PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL
AND PHYSICAL SCIENCES OF THE PACIFIC REGION

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CONTENTS

Late Cenozoic Ostracodes from the Drowned Terraces in the Hawaiian Islands

JOHN C. HOLDEN[1]

ABSTRACT: Late Cenozoic ostracodes from extensive submarine terraces in the Hawaiian Islands ranging in depth from 260 to 355 fathoms resemble, in part, modern shallow water faunas of the Hawaiian and tropical Pacific islands. Of the 35 species from the terraces, 13 are described as new. These are: *Cytherelloidea monodenticulata, Bairdia kauaiensis, B. hanaumaensis, B. ritugerda, Hemicythere obesa, Mutilus oahuensis, M.(?) coalescens, Jugosocythereis venulosus, Quadracythere hornibrooki, Loxoconcha batei, L. condyla, Cletocythereis bradyi,* and *Neocaudites terryi.*

The assemblage indicates an original shallow water environment for the terraces. Most of the extant species, which also occur as fossils from the terraces, live at depths less than 50 fathoms in present oceans, and only one is reliably reported as living deeper than 160 fathoms; several are known littoral forms.

SUBMARINE TERRACES occur at various depths on the flanks of the larger islands in the Hawaiian archipelago. The central islands of Oahu, Molokai, Lanai, Maui, and Kahoolawe surmount a common ridge which rises abruptly from the Pacific Ocean floor from 2,500 fathoms to about 300 fathoms. The conspicuous break in slope at 300 fathoms marks the outer edges of extensively developed drowned terraces (Fig. A). Submarine terraces on the north side of Kauai at about the same depth are not as extensively developed as those off the central islands. Deeper terraces are known down to 1,000 fathoms in the Hawaiian Islands (Menard et al., 1962) but have not yet been dredged.

This study is primarily concerned with the ostracode remains contained in several dredge hauls taken from the submarine terraces within the central island complex and off Kauai. While this is primarily a taxonomic study, Tables 1 and 2 are given to evaluate paleoenvironments and thus unravel the obscure history of the Hawaiian Islands. Unfortunately, such evaluation is hindered by the lack of knowledge of the precise age of the Hawaiian fossil Ostracoda

and of the ecology of living Pacific ostracodes included in this report.

Cursory observations of Recent samples from Clipperton Island and New Caledonia reveal no gross faunal similarities to the Hawaiian fossil faunas. From the limited number of Recent samples from the Hawaiian Islands it can be seen that only a few of the fossil species are presently living in that area (Table 1). Some specimens from the Recent stations are illustrated for clarity.

Marked faunistic differences occur between terraces, indicating either temporal or environmental distictions. For example, station T-12 at 308 fathoms does not contain *Macrocypris gracilis* or *Loxoconchella honoluliensis,* which are common at stations T-1, T-4, and T-7 at 310, 280, and 297 fathoms respectively, nor does it contain the common *Mutilus (?) coalescens* and the abundant *Mutilus oahuensis,* found at station AR at 260 fathoms.

BRIEF HISTORIC REVIEW OF THE OSTRACODA IN THE TROPICAL PACIFIC: The first published work on tropical Pacific ostracodes was that of G. S. Brady (1868a) in "Fonds de la mer." However, only 1 species was treated in the central Pacific. Ostracodes from Java and Hong Kong were also covered in this series. Of greater

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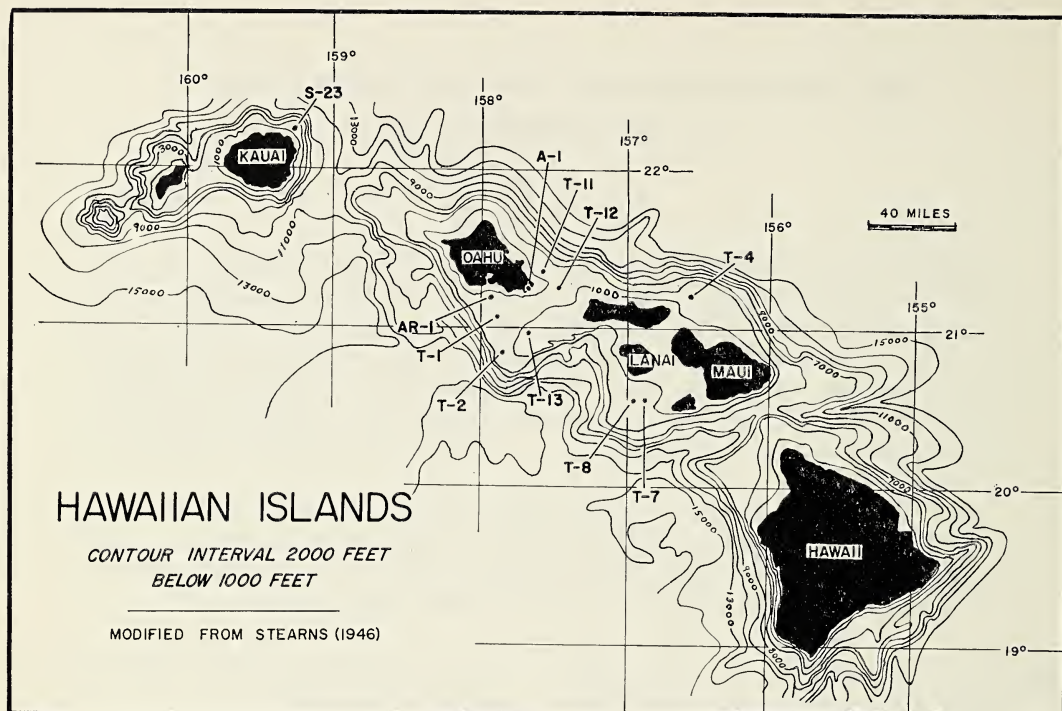
FIG. A. A bathymetric chart of the areas immediately adjacent to the Hawaiian Islands, showing a major break in slope between the 1,000- and 3,000-ft isobath. Stations HA, in Hanauma Bay, and T-13, on Penguin Bank, contain Recent ostracodes exclusively; the remaining stations contain only fossils.

import concerning Pacific faunas was the description of the Ostracoda collected during the Challenger Expedition, also by G. S. Brady, published in 1880. This was primarily a taxonomic treatment of the ostracodes obtained from dredgings in many parts of the world by the Challenger Expedition during the years 1873–1876. Though an excellent work in certain respects, and well illustrated, it was little better than a reconnaissance.

Brady again published in 1890 on the Ostracoda from some South Sea islands (New Caledonia, Samoa, and Fiji). His entire collections consisted of species found from the littoral zone to 6 fathoms. Though certainly not a comprehensive study of South Pacific ostracodes, this, together with his 1880 work, constitutes the bulk of descriptive information available on this group in the tropical Pacific.

J. Th. Kingma (1948) described 94 species, 40 of which were new, from Tertiary to Recent deposits of the Netherlands East Indies. He reported relatively few tropical Pacific island ostracodes living in the Java Sea. Shorter works

in the Indo-Pacific realm include studies of late Cenozoic fossils by Le Roy (1939, 1941) and Doeglas (1931), and of Recent ostracode studies by Chapman (1902, 1910), Triebel (1954), Keij (1953, 1954), 1964), Fyan (1916), and Bold (1946b, 1950).

Major contributions have been made in the New Zealand and the South Australian regions; however, these faunas are distinct from those of the tropical Pacific region. For an historical discussion of that area the reader is referred to Hornibrook (1952). The history of ostracode study in the north Pacific–Japan area is treated thoroughly by Hanai (1959).

AGE AND PALEOECOLOGY: Menard, Allison, and Durham (1962) interpreted the age of a single station (AR of this study) to be probable Late Miocene on the basis of the ratio of extinct coral species to living species and on vagaries in shape of specimens of *Globigerinoides quadrilobatus.* The hermatypic corals indicated an initial depth of only 10 m. Allison (personal communication) has since expressed

TABLE 1

SPECIES CHECK LIST OF LATE CENOZOIC HAWAIIAN OSTRACODES FROM THE HAWAIIAN ISLANDS, CLIPPERTON ISLAND, AND EASTER ISLAND

Relative abundances are made with reference to the total population: 0–5% rare (R); 5–15% common (C); 15–40% abundant (A); 40–100% very abundant (VA).

SPECIES	EASTER ISL.	HAWAIIAN ISLANDS												EASTER ISL.	CLIPPERTON ISL.
		NEOGENE										RECENT			
	EA-2	T-1	T-2	T-4	T-7	T-8	T-11	T-12	AR	S-23	T-13	HA	EA-1	CL
Cytherelloidea monodenticulata n. sp.								R						
Bairdia kauaiensis n. sp.	—	A	VA	C	A	A	VA	A	A	A	A			C
Bairdia sp.									R					
Bairdia honaumaensis n. sp.							R	C				R		
Bairdia ritugerda n. sp.		C	VA	VA			C	C	R					
Bairdia attenuata Brady, 1880		R			R		C	R	C	C		R		
Bairdia expansa Brady, 1880								R						
Macrocypris gracilis (Brady), 1890	R	C		A	A									R
Propontocypris simplex (Brady), 1880	R							R						
Propontocypris(?) sp.								R						
Bythoceratina monstruosa n. sp.	C						R	R		R				
Paracytheridea sp.								R						
Hemicythere obesa n. sp.							R	R						
Hemicythere sp.		R					R	R						
Mutilus (M.) oahuensis n. sp.									A					
Mutilus(?) coalescens n. sp.									C	C				
Jugosocytheris venulosus n. sp.							R	R						
Quadracythere hornibrooki n. sp.			C				R	C						
Loxoconcha bati n. sp.		R			C		C	R		R				
Loxoconcha condyla n. sp.								R			R	C	R	
Loxoconcha longispina Key, 1953		C					C	A			R		R	
Loxoconchella honoluliensis (Brady), 1880		C		C	A						R		R	
Loxoconchella anomala (Brady), 1880		R		C	R		C	C		R				
Loxoconcha sp.								R						
Paradoxostoma sp. A								R						
Paradoxostoma sp. B								R						
Paradostoma cf. P. rubrum Muller, 1894			C											
Sclerochilus sp. A								R						
Sclerochilus sp. B								R						
Cletocythereis bradyi n. sp.	C							R						
Hermanites sp.					C									
Neocaudites terryi n. sp.								R						
Xestoleberis nana Brady, 1880		C	A	A	A	VA	C	C	C	C	R	R		
Anchistrocheles fumata Brady, 1890								R						
"Cythere" caudata Brady, 1890		R											R	
TOTAL NUMBER OF OSTRACODES	110	32	14	15	45	7	49	493	34	35	63	350	60	87

reservations about the age assessment due, primarily, to the occurrence of *Globorotalia truncatulinoides*. The sample from the deepest station of the present study, station S-23 from the north side of Kauai at 355 fathoms, contains many specimens of *Globorotalia truncatulinoides*, which is considered to be of Pliocene to Recent age (Geiger, 1962; Todd, 1964). Station S-23, unlike the other stations, is lithologically distinct, being composed of alternating fine beds of calcareous sand and volcanic ash; hence, the foraminifers obtained from the sand are contemporaneous with deposition. The lack of Miocene and older foraminifers also suggests that the terraces are probably no older than Pliocene. Unfortunately, a definite age cannot be assigned at present to any of the terraces, and all must be considered here as Neogene to possibly Pleistocene, or late Cenozoic.

Ostracodes previously described and dealt with here are mostly South Pacific forms. All are found living at depths far shallower than the present depths of the terraces. Information concerning ostracodes with known depth distributions is summarized in Table 2. It is interesting to note that most have been found exclusively in water shallower than 50 fathoms. None of the Recent ostracodes from the drowned terraces are deep water forms; all occur in water less than 160 fathoms deep, with the exception of a single valve of *Bairidia attenuata* from 370 fathoms off the west coast of Africa (Egger, 1901). Unfortunately, very

TABLE 2

KNOWN DEPTH DISTRIBUTIONS IN FATHOMS OF SOME OSTRACODES FROM THE DROWNED TERRACES IN THE HAWAIIAN ISLANDS

SPECIES	PORT JACKSON, AUSTRALIA	TORRES STRAITS, AUSTRALIA	BOOBY ISLAND	"NEAR STATION 305" BRADY, 1880	NEW CALEDONIA	"STATION 167" NEW ZEALAND BRADY, 1880	FRIENDLY ISLANDS	SAMOA	FIJI	HAWAIIAN ISLANDS	CLIPPERTON ISLAND	CORONADO ISLANDS	BAY OF NAPLES	ASCENSION ISLAND	EASTER ISLAND
Bairdia kauaiensis n. sp	2-10	155	6-8	160	3-6				LIT.	22-40					22-55
Bairdia hanaumaensis n. sp.										5, 40					
Bairdia attenuata Brady, 1880		155								5, 40					
Bairdia expansa Brady, 1880									LIT.	40					
Macrocypris gracilis (Brady), 1880									LIT.		20-22				
Pontocypris simplex (Brady), 1880														7	
Bythoceratina monstruosa n. sp.												5			
Loxoconcha condyla n. sp.										5, 22					22-55
Loxoconcha longispina Key, 1953					LIT.				4	22-40					22-55
Loxoconchella honoluliensis (Brady), 1880					2-6			LIT.	LIT.	22-40					22-55
Loxoconchella anomala (Brady), 1880					3-6				LIT.	40					
Paradoxostoma cf. *P. rubrum* Müller, 1880													?		
Cletocythereis bradyi n. sp.						150				22					
Xestoleberis nana Brady, 1880							18			5, 22					
Anchistrocheles fumata Brady, 1890								LIT.							
"Cythere" caudata Brady, 1890									4	5					

little is known of the maximum depth-distributions of these living species and definite conclusions cannot be made about the initial depth of formation of the terraces. However, these assemblages do suggest shallow water environments of deposition and support an extrapolation of the paleoecological findings of Menard et al. at Station AR to the other terraces.

The apparent lack of modern sediments on the drowned terraces indicates that they are non-depositional realms, at least in part, and may have been exposed since the time of their formation. The fossil assemblages, therefore, may represent a mixture of various ages. Because of the present extreme depths this possible mixture would not be expected to contain living ostracodes, at least not of the shallow water forms treated here. The lack of well preserved specimens lends support to the view that all are fossil occurrences.

In Table 2, occurrences of known and new species are reported from Easter Island, Clipperton Island, and from depths shallower than 40 fathoms in the Hawaiian Islands. The remaining stations are those of Brady (1880, 1890) and Müller (1894). Depths listed as littoral refer to "between tide marks" as used by Brady (1890).

Shepard of Scripps Institution of Oceanography, who collected dredge hauls from stations AR and S-23. E. C. Allison offered great assistance in many aspects of this work and contributed samples from stations HA, CL, and EA, as well as having in his charge all the dredge haul samples. Also appreciated were the helpful comments and suggestions made by E. G. Barham and E. L. Hamilton of the U. S. Navy Electronics Laboratory at San Diego, California, and N. J. Ayer, a fellow graduate student at San Diego State College. The paper has benefited greatly from discussions with W. M. Briggs, Jr., of the U. S. Geological Survey, and J. E. Hazel of the U. S. National Museum, who read and offered many helpful suggestions on the final draft. R. H. Bate of the British Museum (Natural History) kindly compared specimens of several of the species with G. S. Brady's types. Mr. Ayer, presently at the University of Illinois, proof-read the final draft.

DISCUSSION OF THE STATIONS

Several oceanographic expeditions have dredged the submarine terraces in the Hawaiian island chain during the past few years. The most informative sample from station AR of this paper was collected September 2, 1961 by V. W. Menard of Scripps Institution of Oceanography aboard the Scripps Institution's R. V. "Argo."

During March 26–31, 1962, thirteen dredge hauls were collected at various locations from the drowned terraces by R. D. Terry of the Autonetics Division of North American Aviation Corporation at Anaheim, California, aboard the U.S.S. "Greenlet." Of the dredge hauls obtained in this series, most of which consisted of coral fragments, eight contained rocks bearing fossil ostracodes. The dredge haul from Station T-13 of the same series was not collected from a drowned terrace but from Penguin Bank, at a depth of only 22 fathoms, and contained only Recent ostracodes.

The most recently recovered dredge haul from the area, Station S-23 of Francis P. Shepard of Scripps Institution of Oceanography, was taken aboard the Scripps Institution's R. V. "Spencer F. Baird" on September 9, 1962. Unlike the previous dredge hauls by Menard and

Terry, Shepard's was from a deeper terrace on the northeast side of the island of Kauai at 355 fathoms. This terrace is not connected with the terrace complex of the central islands but is separated by a depth of about 1,600 fathoms.

The sample from Clipperton Island (station CL) was collected by E. C. Allison and C. Limbaugh during the Scripps 1956 AGE Expedition. Material from station HA from Hanauma Bay in the Hawaiian Islands was collected by E. C. Allison in 1961. The above Recent stations are in relatively shallow water and specimens were obtained using SCUBA diving equipment.

The Recent station notations (except for Station T-13, which is part of the series collected by R. D. Terry), and including Stations CL and HA have been established by the writer. Notations AR, EA-1, and EA-2 are used here for the fossil stations established by Menard, et al. (1962) and during the Downwind expedition, respectively. In the following paragraphs the locations, bathymetry, and general physiography of each station are given together with any available information about the samples.

Station T-1. A dredge haul from 21° 9.4′N, 157° 54.6′W at 300 fathoms to 21° 7.3′N, 157° 54.4′W at 310 fathoms across the top of a terrace. A small coarse fraction was screened from light-tan coraline muds.

Station T-2. A dredge haul from 20° 51.8′N, 157° 54.7′W at 340 fathoms to 20° 52.2′N, 157° 53.6′W at 240 fathoms, up to the edge of a terrace. About 20 lb of basalt heavily encrusted with MnO_2, several manganese nodules, and fossil reef material were collected.

Station T-4. A dredge haul from 21° 16.2′N, 156° 34.3′W at 280 fathoms to 21° 16.0′N, 156° 34.1′W at 278 fathoms, across the outer edge of a terrace. About 10 lb of fossil reef material were collected.

Station T-7. A dredge haul from 20° 33.3′N, 156° 54.4′W at 297 fathoms to 20° 34.9′N, 156° 52.9′W at 221 fathoms, across the top of a terrace. Total sample consisted of a quarter-pound rock specimen of calcareous algae with fossil material filling the cavities.

Station T-8. A dredge haul from 20° 34.7′N, 156° 54.5′W at 275 fathoms to 20° 34.3′N, 156° 55.8′W at 318 fathoms, across the top of

a terrace. The total sample consisted of two small rocks of calcareous algae.

Station T-11. A dredge haul from 21° 22.8′N, 157° 34.7′W at 295 fathoms to 22° 23.1′N, 157° 33.8′W at 320 fathoms across the top of a terrace. About 30 lb of reef rock, some fragments with MnO_2 coatings, and some basalt pebbles were collected.

Station T-12. A dredge haul from 21° 17.8′N, 157° 28.8′W at 308 fathoms to 21° 19.0′N, 157° 29.7′W at 322 fathoms across the top of a terrace. About 150 lb of reef rock similar to T-11 were collected.

Station T-13. A dredge haul from 20° 59.5′N, 157° 42.0′W at 22 fathoms to 20° 59.5′N, 157° 41.8′W at 22 fathoms, across the top of Penguin Bank. About 200 lb of living reef material were collected.

Station S-23. A dredge haul collected in September 1962 by Francis P. Shepard aboard the Scripps Institution's R. V. "Spencer F. Baird" at 22° 13.6′N, 159° 16.6′W at 355 fathoms, on a drowned terrace on the north side of Kauai.

Station HA. A bottom sample collected in August 1962 by Edwin C. Allison at 157° 41.8′W, 21° 16.5′N at 10 m in Hanauma Bay, on the southeast corner of Oahu, consisting of about 1 lb of clean calcareous sand containing living ostracodes.

Station AR. A dredge haul collected by Henry W. Menard aboard the Scripps Institute's R. V. "Argo" at about 21° 14′N, 157° 57′W at about 260 fathoms from a drowned terrace off Honolulu, Hawaii. More than 200 lb of fossil reef debris were collected.

Station CL. A bottom sample collected in August 1948 by Edwin C. Allison off the edge of a submerged terrace on the north side of Clipperton Island, opposite the west end of the main washout area, at 20–22 fathoms. Sample contained living ostracodes.

Station EA-1. A dredge haul collected in February 1958 during the Scripps Institute of Oceanography's Downwind Expedition at 27° 04′S, 109° 18′W at 22–25 fathoms in La Perouse Bay, Easter Island. The sample contained 200 lb of basalt cobbles and calcareous debris and living coral.

Station EA-2. A dredge haul collected in February 1958 during the Scripps Institute of Oceanography's Downwind Expedition at 27° 04′S, 109° 16′W at 72–80 fathoms. The sample contained 50 lb of living corals and mollusks around fossiliferous limestone and marl.

SYSTEMATIC DESCRIPTIONS

Following each locality number in the species-distribution section is the absolute abundance of that species; the number of single valves observed is denoted by "valves," entire specimens by "entire." All measurements are in millimeters.

Most of the types are reposited at the U. S. National Museum in Washington, D.C. and are designated with USNM numbers. Some secondary types are reposited at the San Diego Museum of Natural History in San Diego, California, and are designated with SDNH numbers (San Diego Natural History Society).

Subclass OSTRACODA Latreille, 1802
Order PODOCOPIDA Müller, 1894
Suborder PLATYCOPINA Sars, 1866
Family CYTHERELLIDAE Sars, 1866
Genus *Cytherelloidea* Alexander, 1929

Cytherelloidea monodenticulata n. sp.
Figs. 1 *a–e*

DIAGNOSIS: Randomly pitted carapace; faint circular central depression in adult, and large centrodorsal toothlike structure in left valve.

DESCRIPTION: In lateral view: carapace slightly narrowing posteriorly; dorsal margin gently convex; ventral margin broadly, gently concave; anterior margin evenly rounded; posterior margin truncate (mature) to rounded (immature); greatest height at anterior; broad rim around all margins, except mid-dorsum, bounded by deep pits (mature) or large reticulations (immature); anteromarginal rim with narrow peripheral ridge, tending to be denticulate in adults; surface of left valve sparsely pitted in low areas, more densely pitted near margins, surface of right valve in penultimate instar smoother than left valve; oblong subcentral depression prominent; dorsal and elongate posterodorsal depression poorly developed. In dorsal view: greatest width just behind center.

Right valve larger and overlapping left valve; strong toothlike projection present in
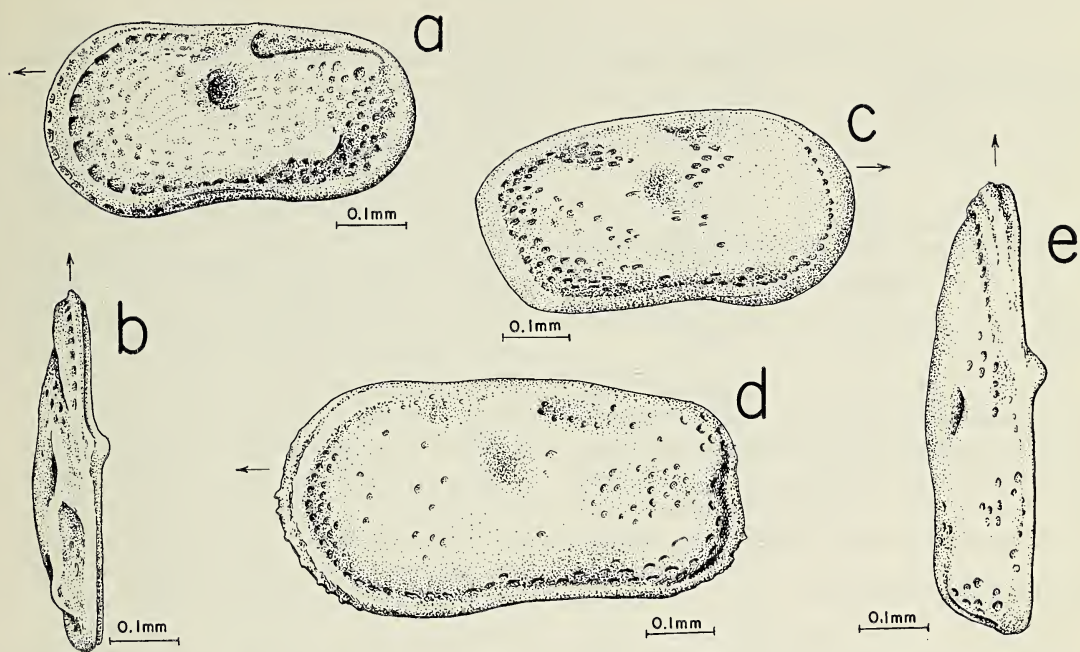
FIG. 1. *Cytherelloidea monodenticulata* n. sp. *a–b,* Paratype SDNH 1025; *a,* side view of penultimate left valve; *b,* dorsal view showing toothlike structure. *c,* Paratype USNM 648713; side view of penultimate right valve. *d–e,* Holotype USNM 648712; *d,* side view of adult female left valve; *e,* dorsal view showing toothlike structure.

mid-dorsum of left valve and equally well developed in penultimate instars; internal features not observed.

DIMENSIONS:

SPECIMEN	LENGTH	WIDTH	HEIGHT
Holotype USNM 648712 (left valve, adult ♀) T-12	0.67	0.15	0.35
Paratype USNM 648713 (right valve, young) T-12	0.58	0.10	0.32
Paratype SDNH 1025 (left valve, young) T-12	0.56	0.10	0.30
Paratype USNM 648714 (left valve, young) T-12	0.52	0.10	0.30

DISTRIBUTION: As fossils from T-12 (14 valves).

DISCUSSION: The prominent toothlike structure in the mid-dorsum of the left valve is distinctive; apparently it is a persistent feature occurring in both adult and penultimate instars. *Cytherelloidea* sp. of Keij (1953:156) from the Banda Sea, Netherlands East Indies, also shows a prominent tooth although it is not conspecific with *C. monodenticulata* n. sp. Van den Bold (1963) reviews this phenomenon in other species in the genus.

The fairly smooth exterior, uncontorted by conspicuous depressions save for a subcentral depression, sets this species apart from the great majority of Indo-Pacific *Cytherelloidea,* such as those dealt with by Le Roy (1941), Brady (1880), Kingma (1948), and Keij (1964).

The specific name refers to the single toothlike structure near the mid-dorsum.

Suborder PODOCOPINA Sars, 1866
Superfamily BAIRDIACEA Sars, 1888
Family BAIRDIDAE Sars, 1888
Genus *Bairdia* McCoy, 1844

REMARKS: Sohn (1960:7, 12) points out that more than 600 species of *Bairdia* have been described from Ordovician to Recent ages, but that sexual dimorphism, at least of the hard parts, has gone unnoticed. Kornicker (1961) has shown, however, that certain living species of the genus from the Caribbean have taller males. Similar dimorphism apparently occurs in species of the present study.
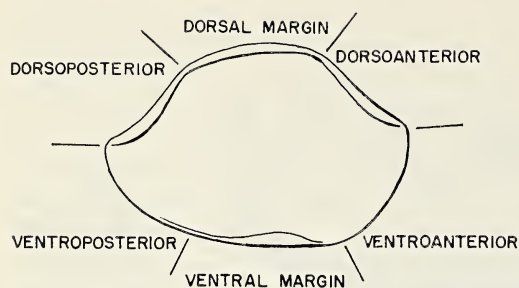
FIG. 2. Terminology of the lateral outline of the genus *Bairdia* (adopted from Sohn, 1960).

Carapace terminology of the *Bairdia* lateral outline has been adopted from Sohn. Unlike the cytheracid carapace, *Bairdia* does not have a posterior and anterior margin per se, these being more conveniently considered as continuations of the dorsal and ventral margins, respectively.

Bairdia kauaiensis n. sp.
Figs. 3 *a–i*

Bairdia amygdaloides Brady, 1880. Rept. Voyage *Challenger*, Zool. 1, pp. 54–55, pl. 9, figs.

DIAGNOSIS: Large, somewhat posteriorly-pointed carapace, greatly and evenly inflated; smooth to finely pitted surface; and similarly shaped anterior and posterior vestibules.

DESCRIPTION: Carapace large (maximum length about 1.2 mm); left valve overlapping right valve except at pointed caudal process; ventral and dorsal margins broadly, evenly rounded. Right valve: dorsoposterior slightly concave, sloping about 40°; dorsal margin straight to slightly convex, sloping about 10–15°; dorsoanterior straight, sloping about 30°; ventral margin gently concave; ventroanterior bluntly rounded; ventroposterior slightly concave, entire surface densely but faintly pitted.

Hinge typical for genus; adductor muscle scar pattern of about eight or nine smaller scars, basically five scars encircling a larger scar with two scars below these; two small mandibular scars anterior to lower adductor scars.

Anterior and posterior vestibules equally large, with about same proportions; radial pore canals fairly abundant, straight, simple.
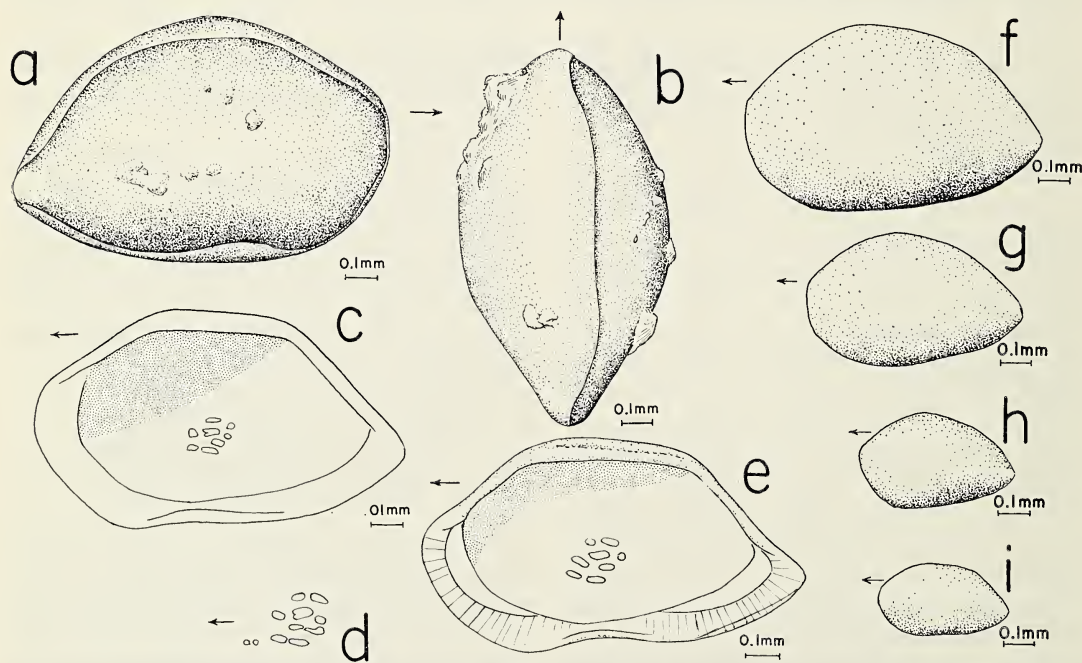
FIG. 3. *Bairdia kauaiensis* n. sp. *a–b*, Holotype USNM 648719; *a*, lateral view of female right valve showing overlap of left valve; *b*, dorsal view. *c*, Paratype SDNH 1026; internal view of male right valve. *d*, Paratype USNM 648720; muscle scar pattern of right valve. *e*, Paratype USNM 648721; internal view of male right valve. *f*, Paratype SDNH 1027; penultimate left valve. *g*, Paratype SDNH 1028; left valve of third from last instar. *h*, Paratype SDNH 1029; left valve of fourth from last instar. *i*, Paratype SDNH 1030; left valve of fifth from last instar.

TABLE 3

DIMENSIONS OF *Bairdia kauaiensis* N. SP.

SPECIMEN	LENGTH	WIDTH	HEIGHT
Holotype USNM 648719 (entire ♂) T-12	1.20	0.67	0.78
Paratype SDNH 1026 (right valve ♂) T-12	1.20	0.27	0.70
Paratype USNM 648720 (right valve ♀) T-12	1.26	0.30	0.67
Paratype USNM 648721 (right valve ♀) S-23	1.10	0.28	0.65
Paratype SDNH 1027 (penultimate left valve) T-12	0.94	0.30	0.58
Paratype SDNH 1028 (3d from last left valve) T-12	0.68	0.23	0.41
Paratype SDNH 1029 (4th from last left valve) T-12	0.47	0.13	0.28
Paratype SDNH 1030 (5th from last left valve) T-12	0.37	0.11	0.22
Paratype USNM 648722 (left valve ♂) T-12	1.23	0.45	0.80

DIMENSIONS: See Table 3.

DISTRIBUTION: As fossils from T-1 (8 valves; 2 entire), T-2 (10 valves), T-4 (4 valves; 1 entire), T-7 (4 valves; 2 entire), T-8 (1 entire), T-11 (21 valves; 1 entire), T-12 (82 valves; 7 entire), AR (6 valves; 4 entire), and S-23 (10 valves). Reported by Brady (1880) near Australia at Torres Strait, Humboldt Bay, Hawaiian Islands, Booby Island (10° 36′S, 141° 55′E), and by Brady (1890) at New Caledonia and Fiji. In the East Pacific, found living at Clipperton Island at CL (2 entire), and the Hawaiian Islands at T-13 (10 valves).

DISCUSSION: *Bairdia kauaiensis* n. sp. and *B. amygdaloides* of Brady, 1880 are conspecific, differing only in that the fossils show finer pitting than mentioned by Brady. The type specimen of *B. amygdaloides* from Australia described by Brady in 1866 appears to be a form altogether different from the present forms and those identified with *B. amygdaloides* by Brady in 1880. The type of *B. amygdaloides* is only 0.78 mm long, or about the length of the second- to third-from-last instar of the Hawaiian specimens. Brady (1866:364) mentions that it may be a young; however, it does not bear any resemblances to the young of the new species.

Bairdia kauaiensis n. sp. is one of the most commonly occurring ostracodes from the drowned terraces in the Hawaiian Islands. It is present in significant numbers at all stations, including the Recent T-13, but it is absent from the Recent lagoonal assemblage at HA, where *B. hanaumaensis* is common and *B. attenuata* is rare.

Little variation occurs in this species except for sexual dimorphism in mature specimens, with the supposed males being taller. The preserved population is easily grouped into five molt stages. General shape and inflation, characteristic of mature specimens, is also consistent to the fifth-from-last instar.

The large adductor muscle scar pattern has diagnostic reliability, with a rectangular middle scar surrounded by about five other scars and two aligned elongate scars below. Using the adductor muscle scar pattern alone, obvious differences can be seen between *B. hanaumaensis*, *B. attenuata* (the latter having a very small adductor muscle scar group), and the present species.

The species is named for the island of Kauai, in the Hawaiian Islands.

Bairdia sp.
  Figs. 4 *a–d*

DESCRIPTION: Carapace smooth; highly inflated centroventrally. In lateral view: dorsal margin evenly rounded; dorsoanterior straight; dorsoposterior straight to slightly concave; ventral margin gently concave; ventroanterior bluntly rounded; ventroposterior gently concave; valves unequal; caudal process in right valve pointed, ventrodorsally concave; left valve with poorly developed caudal process. In dorsal view: slightly concave between bulbous center and blunt thick ends.

Adductor muscle scar pattern small, near center; of about 7 or 8 smaller scars; vestibules of moderate size; normal and radial pore canals unobserved.

DIMENSIONS:

SPECIMEN	LENGTH	HEIGHT	WIDTH
USNM 648723 (entire ♀) AR	1.10	0.70	0.70
SDNH 1031 (left valve ♂) AR	1.10	0.75	0.40
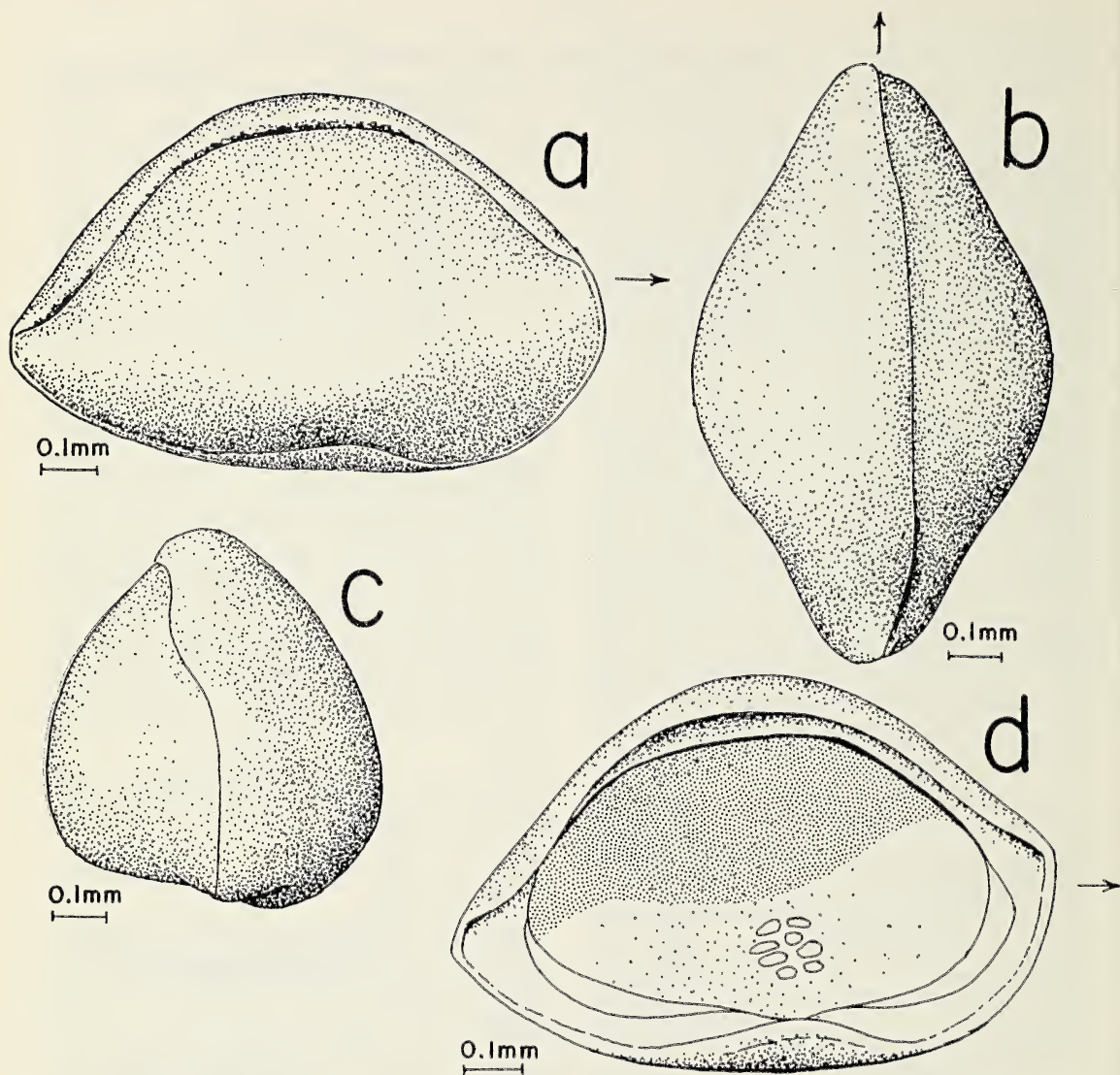
Fig. 4. *Bairdia* sp. *a–c*, Specimen USNM 648723; *a*, lateral right valve view of entire female carapace; *b*, dorsal view; *c*, anterior view. *d*, Specimen SDNH 1031; internal view of male left valve showing ventrally located adductor muscle scar pattern.

DISTRIBUTION: As fossils from AR (1 valve; 1 entire).

DISCUSSION: Initially, this species was thought to be a dimorphic form of *Bairdia attenuata*. Both species have a distinct concavity in the posterodorsum; but this feature is present only in the smaller right valve of *B. pseudofoveolata*. ..*Bairdia* sp. is closely related to *B. foveolata* (*partim*) of Brady (1880), who illustrates two forms under this name which are certainly distinct species. The present species resembles

those of his plate 8, figures 1 *a–f*. Excluding figures 2 *a–f* from this discussion, *B.* sp. is wider in dorsal view, and more ventrally inflated in anterior view, than is *B. foveolata* of Brady, 1880. Brady lists *B. foveolata* as ranging in depth from 7 to 1,150 fathoms. Unfortunately he does not specify at which depths the particular "varieties" of that species occur.

The illustration of *Bairdia bradyi* Bold, 1957 (new name for *B. foveolata* Brady, 1868*b*, not Bosquet, 1852), does not closely resemble those

of *B. foveolata* of Brady (1880, figures 1 *a–f*) or the present species.

Bairdia hanaumaensis n. sp.
Figs. 5 *a–h*

DIAGNOSIS: Finely pitted, centrally bulbous, ventrolaterally inflated carapace with ventral caudal process; elongate-oval in dorsal view.

DESCRIPTION: Carapace elongate, length about twice the height. In lateral view: greatest height anterodorsally; dorsoanterior straight, sloping at about 20°; dorsoposterior straight, sloping at about 50°, ventroposterior and ventral margin continuous, straight; ventro-anterior subtruncate, slightly convex. In anterior view: carapace flattened in dorsal half, highly inflated in ventral half. In dorsal view: sides only slightly convex, subparallel; anterior and posterior blunt; surface appears smooth but under high magnification is densely pitted; living individuals evenly covered with short hairs and are uniformly brown in color.

Adductor muscle scar pattern somewhat variable, usually of nine scars of various sizes and shapes; two antennal scars anterior to lower adductor scars, posterior scar much smaller than other scars; copious mandibular scars just below adductor pattern; several small mandibular scars throughout dorsal half of carapace. Anterior vestibule small; posterior elongate, deepest posteriorly; radial pore canals straight, some bifurcating, with tendency to be paired; hinge typical of genus.

DIMENSIONS: See Table 4.

DISTRIBUTION: As fossils from T-12 (11 valves) and AR (1 valve; 2 entire). Found living at 5 fathoms at HA (15 entire).

DISCUSSION: The low, elongate carapace of *Bairdia hanaumaensis* is distinct from the majority of bairdiids. However, *B. acanthigera* of Brady, 1880 and *B. tuberculata* Brady, 1880 also have this general shape, the former being more comparable to *B. hanaumaensis* than the latter. *B. acanthigera* of Brady, 1880, from 1,070–1,150 fathoms in the North Atlantic, has a more rounded dorsum and ventral margin
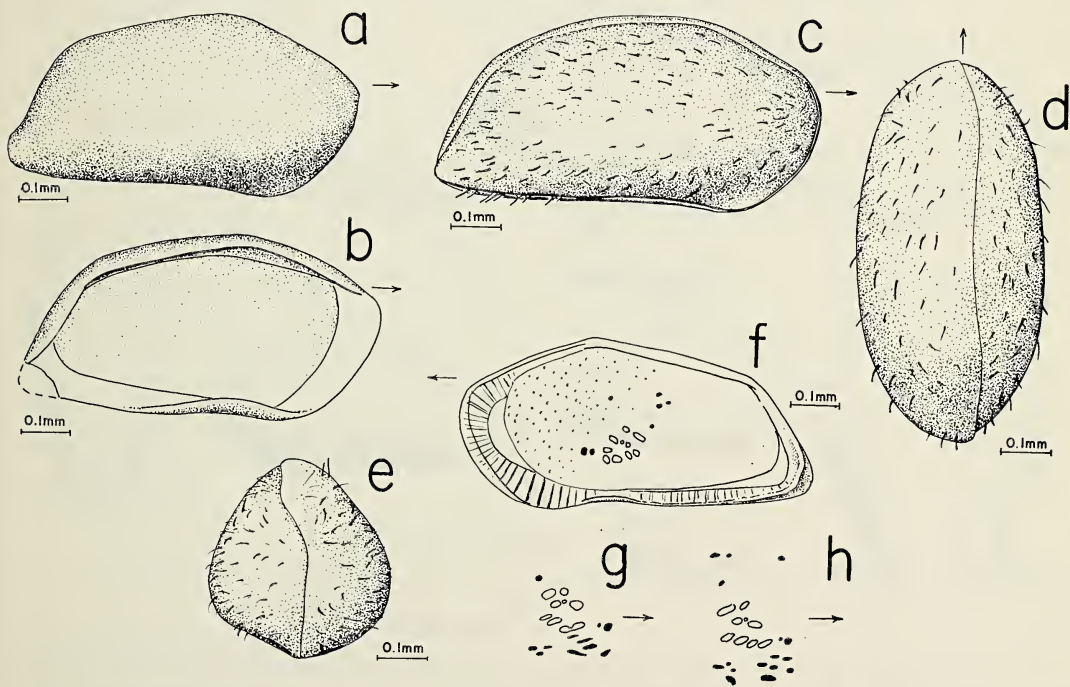
FIG. 5. *Bairdia hanaumaensis* n. sp. *a*, Paratype SDNH 1033; lateral view of right valve. *b*, Paratype USNM 648727; internal view of left valve. *c–e*, Holotype USNM 648724; *c*, lateral view of entire carapace; *d*, dorsal view; *e*, anterior view. *f*, Paratype USNM 648725; internal view of right valve; antennal and mandibular scars in black. *g*, Paratype SDNH 1032; muscle scar pattern from left valve. *h*, Paratype USNM 648726; muscle scar pattern from left valve.

TABLE 4

DIMENSIONS OF *Bairdia hanaumaensis* N. SP.

SPECIMEN	LENGTH	WIDTH	HEIGHT
Holotype USNM 648724 (entire) HA	0.75	0.36	0.37
Paratype USNM 648725 (right valve) HA	0.69	0.16	0.33
Paratype SDNH 1032 (left valve) HA	0.70	0.19	0.36
Paratype USNM 648726 (left valve) HA	0.68	0.19	0.34
Paratype SDNH 1033 (right valve) AR	0.71	0.21	0.37
Paratype USNM 648727 (left valve) T-12	0.69	0.22	0.37
Paratype USNM 648728 (left valve) HA	0.68	0.19	0.36
Paratype USNM 648729 (right valve) T-12	0.68	0.15	0.34
Paratype USNM 648730 (entire) HA	0.68	0.32	0.34

and is not as terminally blunt in dorsal view as *B. hanaumaensis*. The tumid *B. tuberculata* from the Admiralty Islands at 16–25 fathoms, though roughly the same shape, is more distinctly ornate and more inflated. The present species is named for Hanauma Bay, Oahu, Hawaii.

Bairdia ritugerda n. sp.
Figs. 6 *a–g*

DIAGNOSIS: Humped caudal process (terminating with spine in immature specimens), high anterocardinal angle; acuminate posterior; and anteriorly inflated carapace.

DESCRIPTION: In lateral view: carapace pos-
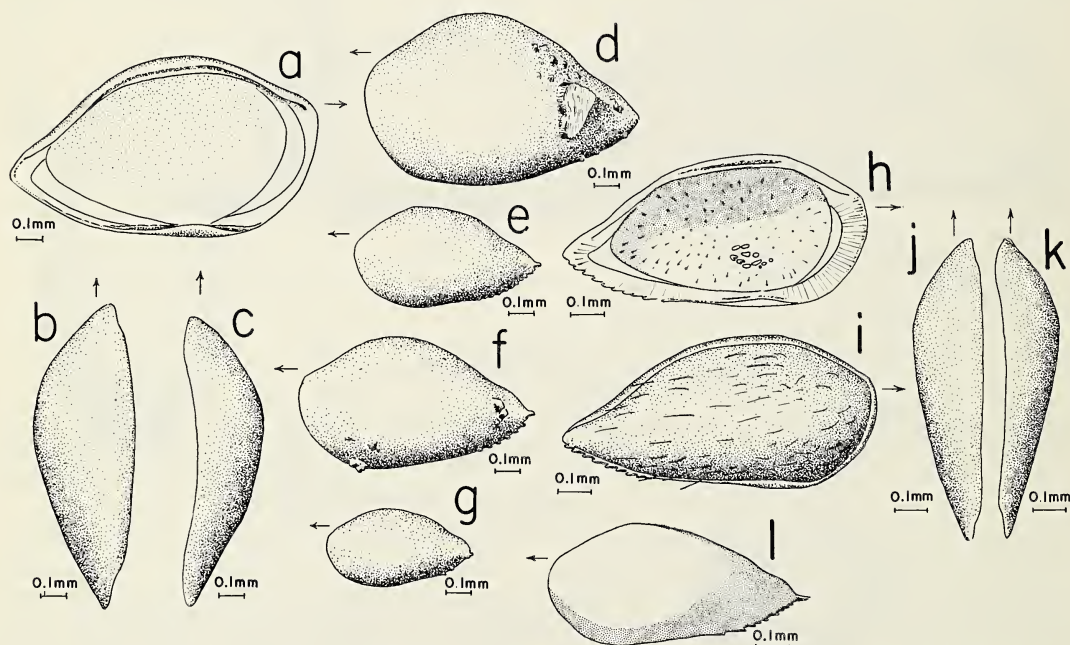
FIG. 6. *Bairdia ritugerda* n. sp. *a–b*, Holotype USNM 648731; *a*, internal view of female left valve showing large vestibules; *b*, dorsal view. *c*, Paratype USNM 648732; dorsal view of male right valve showing concave dorsum. *d*, Paratype SDNH 1034; male left valve. *e*, Paratype SDNH 1035; penultimate left valve showing terminal spine and posteroventral serrations. *f*, Paratype USNM 648733; third from last instar, left valve. *g*, Paratype SDNH 1036; fourth from last instar, left valve. *h–l*, *Bairdia crosskeiana* Brady, 1866; *h–k*, plesiotype USNM 648735; *h*, internal view of left valve; *i*, dorsal view of left valve; *k*, dorsal view of right valve; *l*, plesiotype USNM 648736; penultimate instar showing well-developed terminal spine.

teriorly acuminate; greatest height at anterior part of dorsal margin; dorsoposterior with conspicuous dorsally humped caudal process (terminating with spine in young); dorsoanterior slightly concave, sloping at about 30°; ventral margin gently convex, continuous with straight to slightly convex ventroposterior; ventroposterior serrate in young, some adults with occasional denticles; ventroanterior broadly and gently rounded, subtruncate; surface smooth. In dorsal view: carapace posteriorly acuminate; greatest width, like height, just anterior to midlength; trace of hinge line with left valve broadly arched over right valve.

Duplicature not broad; vestibules large; other internal features obscured.

DIMENSIONS: See Table 5.

DISTRIBUTION: As fossils from T-1 (2 valves; 13 entire), T-2 (6 valves), T-4 (1 valve; 1 entire), T-11 (5 valves; 1 entire), T-12 (28 valves; 10 entire), and AR (1 valve).

DISCUSSION: Other than sexual dimorphism with taller males, little variation occurs in the species. Shape and inflation, characteristic of mature specimens, is also consistent in the young to at least the fourth-from-last instar.

Bairdia gerda Benson and Coleman, 1963, from the west coast of Florida, is quite similar to the present species. *B. gerda* differs from *B. ritugerda* only by the lack of the dorsally humped caudal process, the presence of a straighter venter, and by a more pointed dorsum.

Bairdia crosskeiana Brady, 1866 of Brady 1880 (a misidentification?) is closely related to *B. ritugerda*, as attested by the presence of a well-developed terminal spine in the young, a humped caudal process, and general shape (though much lower than the former species).

Specimens of *B. crosskeiana* of Brady, 1880 found at T-13 are illustrated for comparative purposes (Fig. 6 *h–l*).

Bairdia attenuata Brady, 1880
Figs. 7 *a–d*

Bairdia attenuata Brady, 1880. Rept. Voyage *Challenger,* Zool. 1, pt. 3, p. 59, pl. 11, figs. 3 *a–e.*

Bairdia attenuata Brady. Egger, J. G., 1901, Abh. Math.-Phys. Cl. koninkl Bayer. Akad. Wiss. 21, no. 2, p. 425, pl. 2, figs. 9, 12.

DIAGNOSIS: Posterior and anterior sharply upturned, especially pronounced in left valves; terminally compressed carapace; high, rounded dorsum.

DESCRIPTION: In lateral view: surface faintly pitted; dorsal margin arched; dorsoanterior and dorsoposterior conspicuously concave; anterior margin slightly convex; ventroposterior broadly rounded; ventroanterior broadly rounded in lower part, tightly rounded in upper part. In dorsal view: carapace compressed, diamond shaped; greatest width medially; ends evenly, sharply acuminate; males taller than females.

Adductor muscle scar pattern of about seven small scars encircling a single larger scar; antennal or mandibular scars not observed. Posterior vestibule shallow, anterior vestibule bilobed, shallow; radial pore canals abundant, simple; normal pores minute, dense.

DIMENSIONS:

PLESIOTYPE	LENGTH	WIDTH	HEIGHT
USNM 648737			
(left valve ♀) S-23	1.05	0.33	0.67
SDNH 1037			
(entire ♂) AR	1.12	0.50	0.70
USNM 648738			
(left valve ♀) T-12	1.05	0.32	0.63

TABLE 5

DIMENSIONS OF *Bairdia ritugerda* N. SP.

SPECIMEN	LENGTH	WIDTH	HEIGHT
Holotype USNM 648731 (left valve ♀) T-12	1.17	0.34	0.68
Paratype USNM 648732 (right valve ♂) T-12	1.08	0.24	0.57
Paratype SDNH 1034 (left valve ♂) T-12	1.05	0.34	0.67
Paratype SDNH 1035 (penultimate, left valve) T-12	0.88	0.24	0.50
Paratype USNM 648733 (third from last, left valve) T-12	0.69	0.19	0.40
Paratype SDNH 1036 (fourth from last, left valve) T-12	0.53	0.14	0.30
Paratype USNM 648734 (right valve) T-12	1.00	0.25	0.55
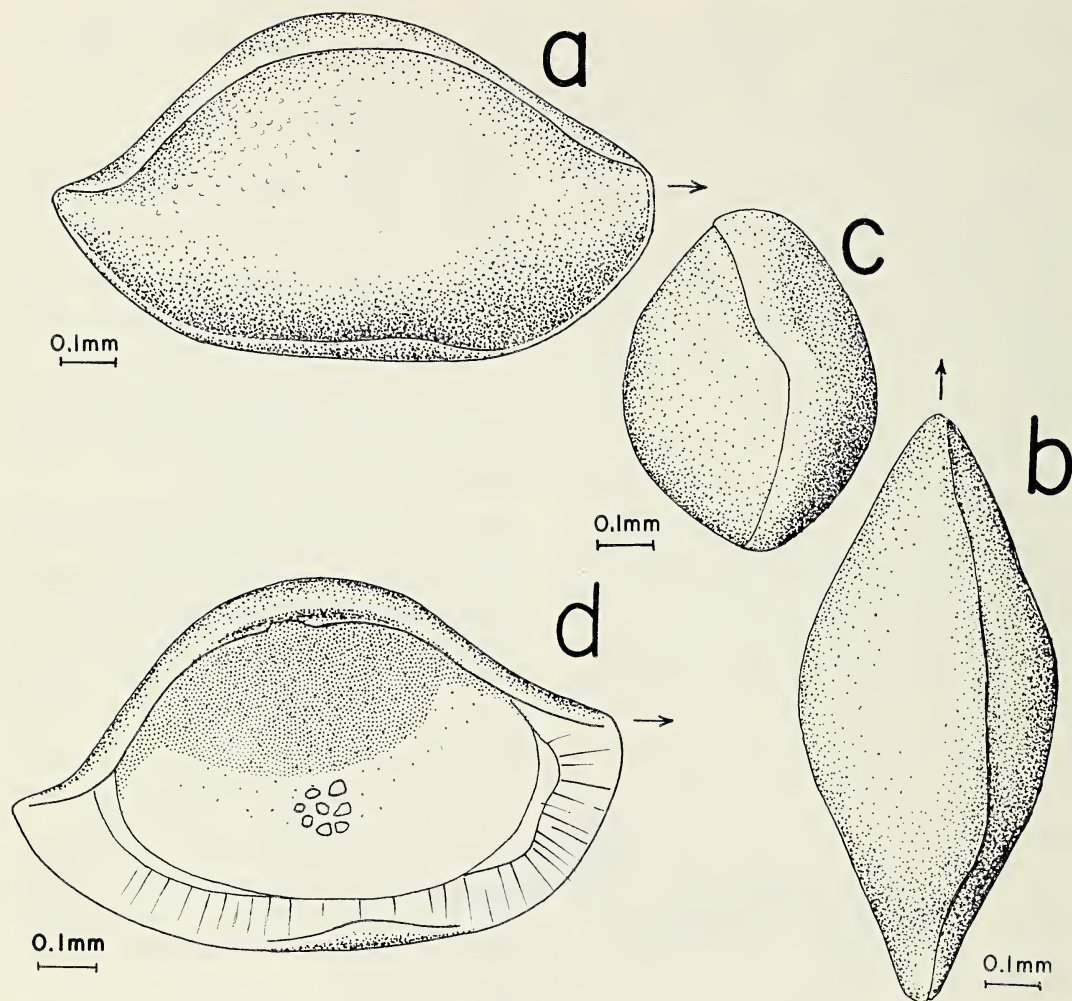
FIG. 7. *Bairdia attenuata* Brady, 1880. *a–c,* Plesiotype SDNH 1037; *a,* right valve of entire male carapace; *b,* dorsal view; *c,* anterior view. *d,* Plesiotype USNM 648737; internal view of female left valve showing adductor muscle scar group.

DISTRIBUTION: As fossils from T-1 (1 valve), T-7 (1 valve), T-11 (2 valves; 3 entire), T-12 (13 valves; 1 entire), AR (1 valve; 1 entire), and S-23 (3 valves). Brady (1880:59) reports this species from two dredgings; one at Torres Straits, 11° 35′S, 144° 3′E, at 155 fathoms, and one near Hawaii at 40 fathoms. As "young Pliocene" fossils from Timor, Netherlands East Indies (Fyan, 1916:78). Found living at HA (1s) at 5 fathoms. Egger (1901) reports a single valve off the west coast of Africa at 370 fathoms (redeposited?).

DISCUSSION: Sexual dimorphism is subtly manifested by a taller male. The similarity of these specimens to *Bairdia attenuata* of Brady (1880) and Fyan (1916) is close, though the Hawaiian specimens dealt with here show a lower caudal process. Brady (1880), when describing the species, apparently illustrated forms not from Hawaii. Dr. Bate (personal communication) of the British Museum (Natural History), who compared some of the present specimens with Brady's types, also notes that the former have a more upturned posterior and anterior. However, similarities in morphology and the nature of the adductor scar pattern, i.e., size, shape, configuration, and position, suggest that these specimens are conspecific with Brady's form.

Bairdia expansa Brady, 1880
  Figs. 8 *a–d*

Bairdia expansa Brady, 1880, Rept. Voyage *Challenger*, Zool. 1, pt. 3, p. 58, pl. 11, figs. 2 *a–e*.

DIAGNOSIS: Small, greatly inflated carapace, compressed in antero-posterolateral regions; high anterocardinal angle; abrupt upturned posteroventer; smooth porcelaneous surface.

DESCRIPTION: In lateral view: carapace greatly inflated midventrolaterally; dorsoposterior concave in posterior part, continuous with broadly rounded dorsal margin; dorsoanterior concave; ventroanterior bluntly rounded, with few scattered denticles; ventral margin straight, convex with ventrally extended inflation; ventroposterior abruptly rounded with several denticulations; surface of carapace smooth, apparently imperforate, with porcelaneous texture. In dorsal view: greatest width medially; laterally compressed at ends giving concave lateral extremities; left valve strongly overlapping right valve.

Duplicature moderately wide. Adductor muscle scar pattern apparently large, of many smaller scars.

DIMENSIONS:

PLESIOTYPE	LENGTH	WIDTH	HEIGHT
USNM 648739			
(adult left valve)			
T-12	0.84	0.34	0.48±
SDNH 1038			
(penultimate left valve)			
T-12	0.70	0.24	0.40

DISTRIBUTION: As fossils from T-12 (3
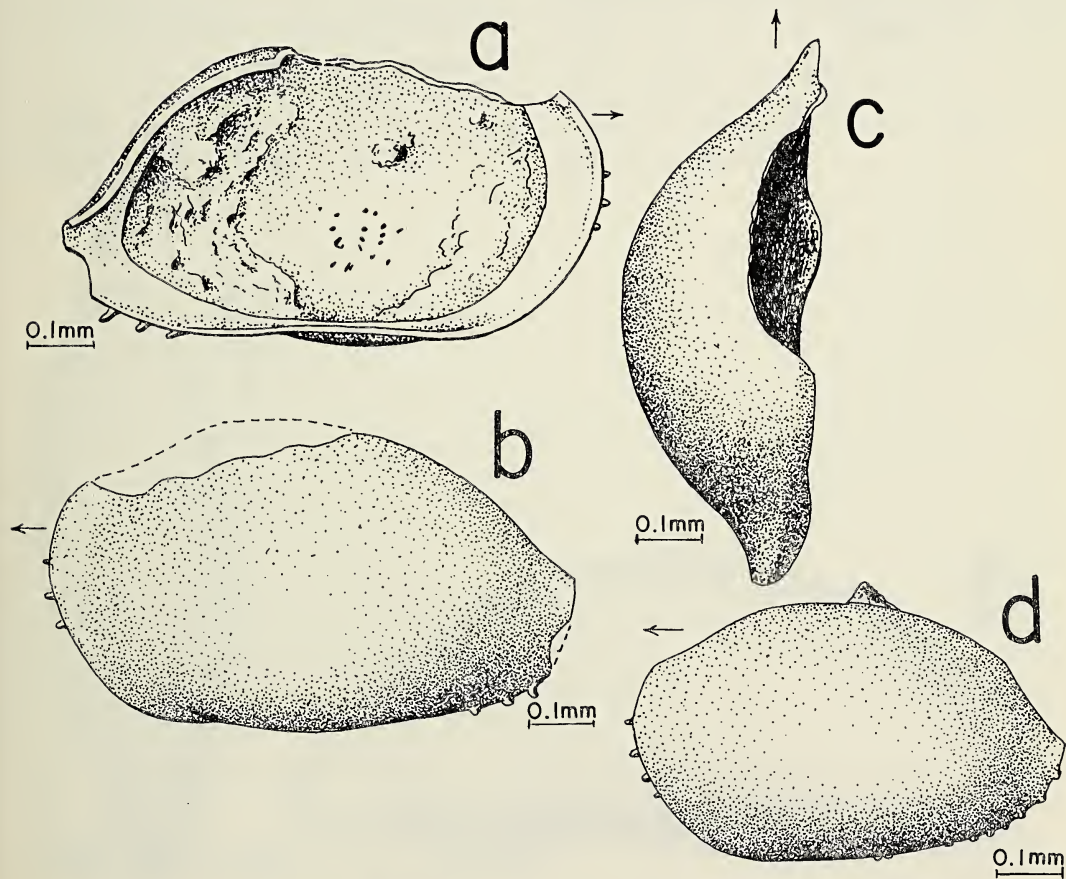
FIG. 8. *Bairdia expansa* Brady, 1880. *a–c*, Plesiotype USNM 648739; *a*, internal view of broken left valve; *b*, lateral view showing dashed line reconstruction; *c*, dorsal view. *d*, Plesiotype SDNH 1038; lateral view of penultimate left valve.

valves). Reported living by Brady (1880) in the Hawaiian Islands at 40 fathoms, and by Brady (1890) from tide pools in Samoa.

DISCUSSION: Brady noted that *Bairdia expansa* occurred with *B. amygdaloides* (=*B. kauaiensis*), and *B. crosskeiana* of Brady, 1880 and *B. attenuata*. Its fossil bairdiid association is somewhat different, being with abundant *B. kauaiensis,* common *B. ritugerda,* rare *B. attenuata* and *B. hanaumaenis. Bairdia crosskeiana* has not been found as a fossil from the Hawaiian Islands.

Macrocypris gracilis (Brady), 1890
    Figs. 9 *a–b*

Pontocypris gracilis Brady, 1890. Trans. Roy. Soc. Edinburgh 35, p. 491, pl. 1, figs. 5–6.

DIAGNOSIS: Low, elongate, inflated carapace; slightly to moderately concave venter; broadly, evenly arched dorsum.

DESCRIPTION: In lateral view: carapace elongate, length about three times the height; right valve overlapping smaller left valve everywhere except at mid-dorsum; dorsal margin broadly but evenly arched; anterior margin rounded, ventrally extended; ventral margin almost straight, slightly concave at midlength; pointed posterior near venter; surface smooth. In dorsal view: carapace narrow, length about three and a half times width; terminally acuminate with equal posterior and anterior angulation. Internal features not observed.

DIMENSIONS:

PLESIOTYPE	LENGTH	WIDTH	HEIGHT
USNM 648715			
(entire) T-4	1.06	0.32	0.39
SDNH 1039			
(right valve) T-4	0.95	0.18	0.39

DISTRIBUTION: As fossils from T-1 (2 valves), T-4 (1 valve: 1 entire), and T-7 (3

FIG. 9. *Macrocypris gracilis* (Brady), 1890. *a–b*, Plesiotype USNM 648715; *a*, lateral left valve view of entire carapace showing overlap of right valve; *b*, dorsal view.

valves; 2 entire), and from Easter Island at EA-2 (3 valves). Found living at Clipperton Island and by Brady (1890) "between tide marks" at Levuka and Rambe islands in the Fiji Islands.

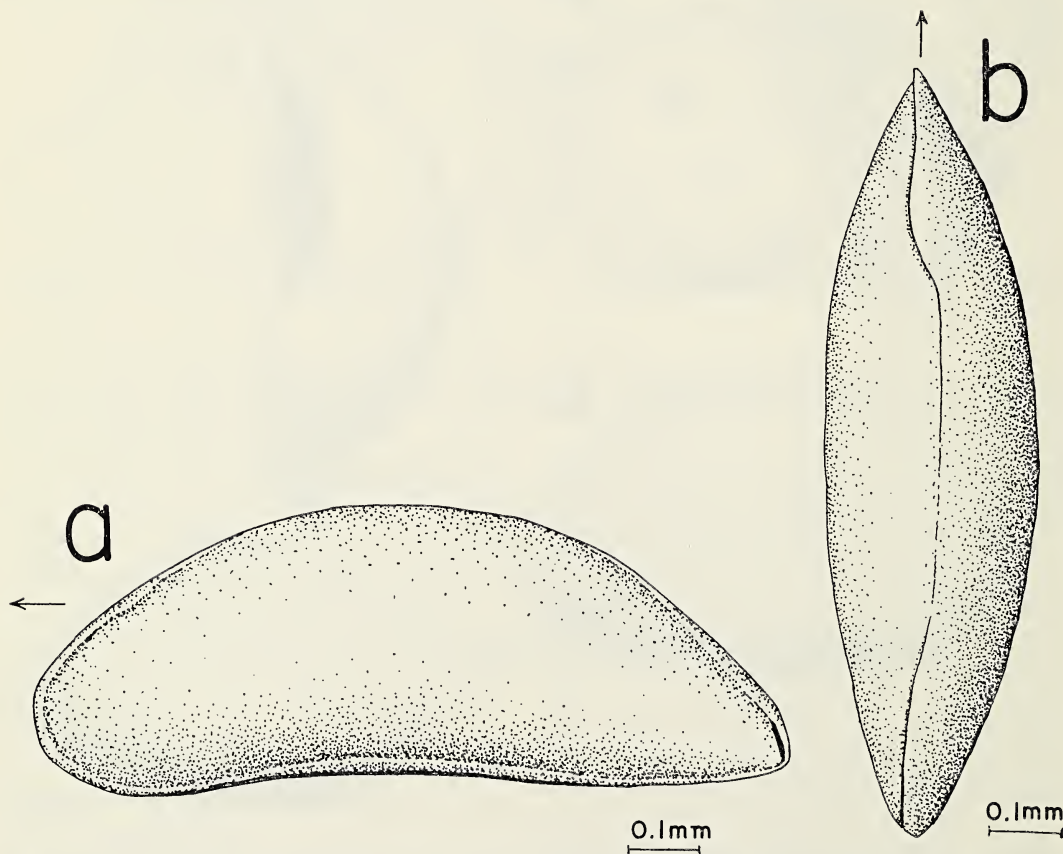DISCUSSION: The size and shape of the Hawaiian specimens appear identical to *Pontocypris gracilis* Brady, 1890 from the Fiji Islands. However, the species is here assigned to the genus *Macrocypris* on the basis of its shape, smooth margins, valve overlap, and affinities to living *Macrocypris* in the Hawaiian Islands as seen by the writer.

The carapace of *Macrocypris* is most readily confused with that of *Paracypris,* but differs primarily by having a larger right valve, distinct dentition, and more abundant adductor muscle scars.

A feature commonly overlooked in discussions of *Macrocypris* is the dorsal overlap of the right valve by the otherwise smaller left valve. This characteristic is apparent in illustrations of the type species and also occurs in *Macrocypris gracilis* (Brady), 1890.

Superfamily CYPRIDACEA Baird, 1845
Family PROPONTOCYPRIDIDAE Müller, 1894
Genus *Propontocypris* Sylvester-Bradley, 1947

Propontocypris simplex (Brady), 1880
Figs. 10 *a–b*

Pontocypris simplex (Brady), 1880. Rept. Voyage *Challenger,* Zool. 1, pt. 3, p. 37, pl. 1, figs. 5 *a–d*.

DIAGNOSIS: Broadly and evenly rounded dorsum; concave anteroventer; laterally flattened valves.

DESCRIPTION: In lateral view: carapace somewhat stout; height almost half the length; dorsal margin broadly arched, greatest height just anterior to middle; anterior margin obliquely rounded, ventrally extended; ventral margin concave in anterior half, convex in posterior half; posterior pointed; right valve larger, overreaching left valve everywhere except at middorsum where left valve overlaps right valve; surface smooth; eye tubercles absent. In dorsal view: width about one-third the length; sides flattened; ends bluntly pointed. Internal features not observed.
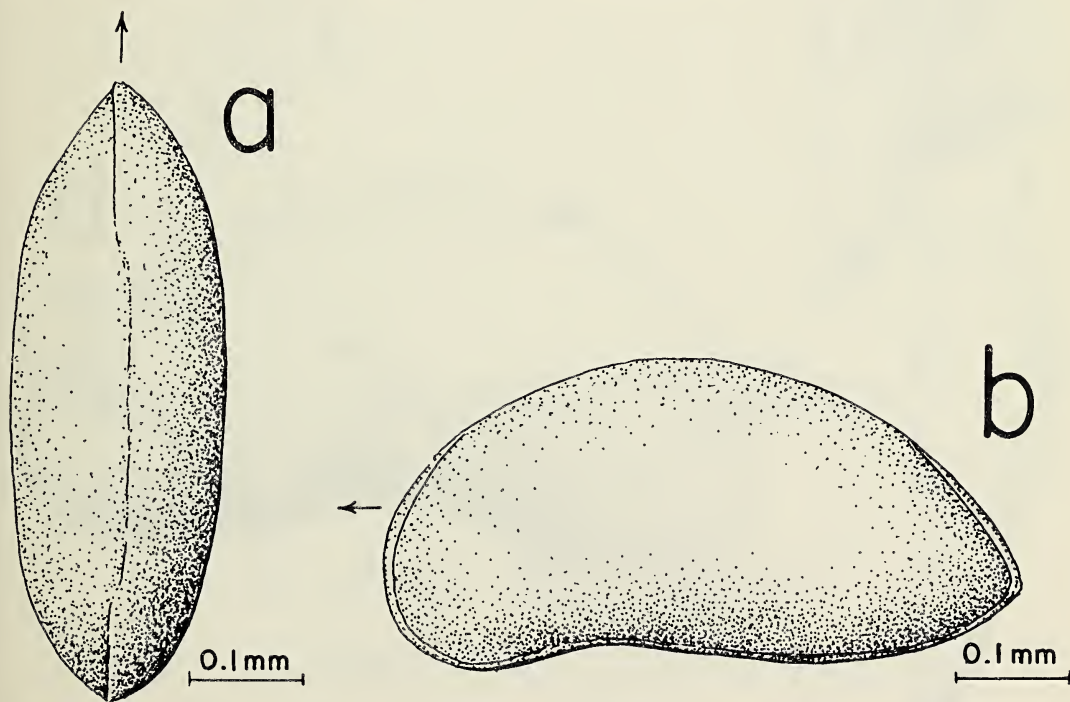
FIG. 10. *Propontocypris simplex* (Brady), 1880. *a–b,* Plesiotype USNM 648716; *a,* dorsal view of carapace showing overlap; *b,* left valve view of carapace showing overlap of right valve.

DIMENSIONS:

PLESIOTYPE	LENGTH	HEIGHT	WIDTH
USNM 648716			
(entire) T-12	0.55	0.26	0.20
SDNH 1040			
(right valve) T-12	0.62	0.24	0.14

DISTRIBUTION: As fossils from T-12 (2 entire) and Easter Island at EA-2 (1 entire). Reported living from 7 fathoms at Ascension Island, South Atlantic by Brady (1880).

DISCUSSION: Only two carapaces were found from the fossil stations in the Hawaiian Islands, but the general shape and nature of valve overlap agrees with Brady's Recent species from the South Atlantic. This is the only report of this species in the Pacific Ocean.

Propontocypris simplex differs from the type species, *Propontocypris trigonella* (Sars), 1866, by having a broadly rounded dorsum, partially concave venter, and a somewhat pointed posterior in lateral view.

Propontocypris(?) sp.
Figs. 11 *a–b*

DESCRIPTION: In lateral view: length about twice the height, greatest height central; dorsum broadly rounded, anterior half evenly rounded, posterior half irregularly rounded; ventral margin greatly concave in anterior three-fourths, convex in posterior quarter; anterior margin evenly rounded, ventrally extended; posterior margin narrowly rounded; right valve apparently overlapping left valve. In dorsal view: carapace narrow, length three times width; terminally acuminate; sides rounded. Internal features not observed.

DIMENSIONS:

SPECIMEN	LENGTH	WIDTH	HEIGHT
USNM 648717			
(left valve) T-12	0.57	0.10	0.30
USNM 648718			
(entire young) T-12	0.47	0.15	0.24
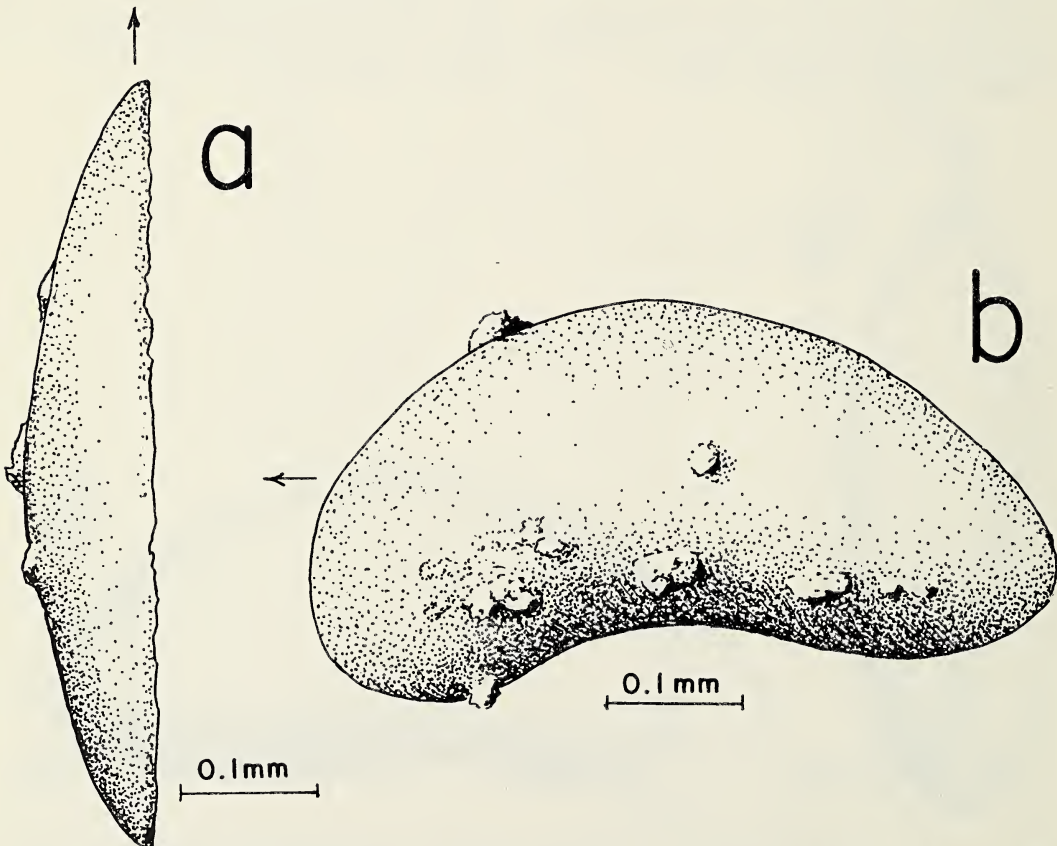
FIG. 11. *Propontocypris* (?) sp. *a–b,* Specimen USNM 648717; *a,* dorsal view of left valve; *b,* lateral view.

DISTRIBUTION: As fossils from T-12 (2 entire; 1 valve).

DISCUSSION: In lateral view the species possesses characteristics of the genus *Paracypris* but, though preservation is poor, it differs from that genus in the important feature of having a larger right valve.

The species is placed in the genus *Propontocypris* primarily on the basis of general shape, but is placed there questionably because of its pronounced concave venter.

Superfamily CYTHERACEA Baird, 1850
Family BYTHOCYTHERIDAE Sars, 1926
Genus *Bythoceratina* Hornibrook, 1952

Bythoceratina monstruosa n. sp.
Figs. 12 *a–d*

DIAGNOSIS: Wide, ornate, massive alae, directed straight back and out at an angle of 30° without a terminal spine; pointed caudal process, grotesque anterodorsal tubercle; surface ornamentation of riblets.
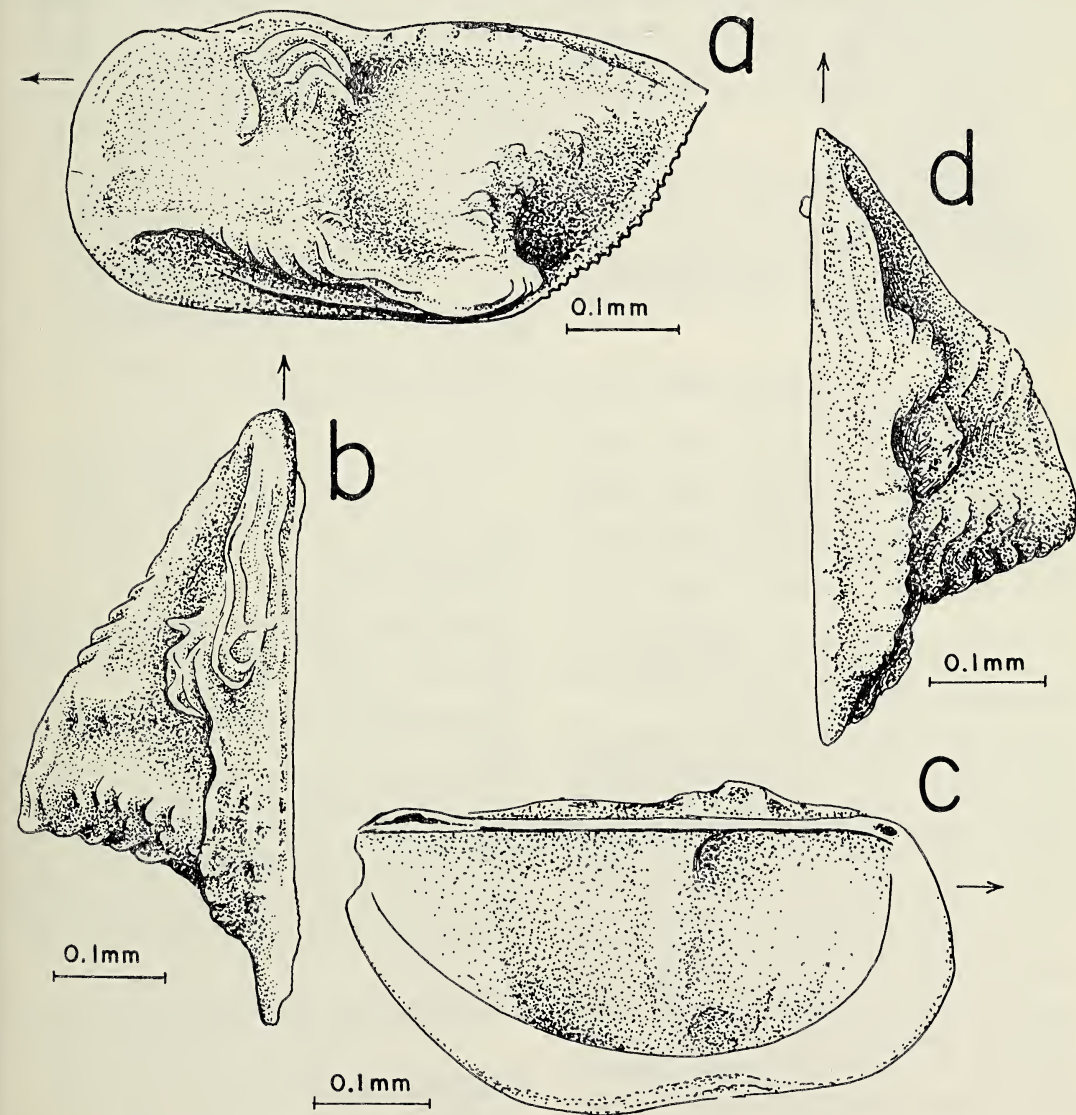
FIG. 12. *Bythoceratina monstruosa* n. sp. *a–b*, Holotype USNM 648740; *a*, side view of left valve; *b*, dorsal view of left valve. *c*, Paratype USNM 648742; internal view of left valve. *d*, Paratype USNM 648741; dorsal view of right valve.

DESCRIPTION: In lateral view: dorsal margin sinuous; anterior margin truncate; ventral margin straight, parallel with dorsal margin, curving up posteroventrally about 45° to high pointed posterodorsal caudal process; oblique posterior margin finely and evenly denticulate. Carapace fragile, small; alar processes large, running from ventral part of anterior margin out and back at about 30° to greater than half the length of carapace; dorsal ridge knobby from pointed posterodorsal caudal process to anterior margin; grotesque tubercle just anterior to deep vertical central sulcus; alae intricately ornamented with sinuous parallel riblets in ventral part developing into many small knobs behind alae.

Hingement lophodont: anterior tooth of right valve small, posterior tooth elongate, inconspicuous; median bar of left valve slightly extended, crenulate at ends, otherwise apparently smooth. Duplicature narrow; other internal features not observed.

DIMENSIONS:

| SPECIMEN	LENGTH	WIDTH	HEIGHT
Holotype USNM 648740			
(left valve) T-12	0.55	0.22	0.27
Paratype SDNH 1041			
(left valve) T-12	0.54	0.22	0.27
Paratype USNM 648741			
(right valve) T-12	0.55	0.22	0.27
Paratype USNM 648742			
(left valve) T-12	0.54	0.21	0.29

DISTRIBUTION: As fossils from T-11 (1 valve), T-12 (13 valves), S-23 (1 valve), and Easter Island at EA-2 (6 valves).

DISCUSSION: This species bears a strong resemblance to two forms from the west coast of North America. One occurrence of a form strikingly similar to *Bythoceratina monstruosa* has been found by the writer in the Coronado Islands 20 miles off San Diego, California. The Recent form is almost identical with the fossil from Hawaii, but differs by having a serrated anterior margin and faint reticulations over most of its surface. Another species of *Bythoceratina* has been observed by the writer in the Pleistocene of Turtle Bay, Baja California, Mexico. These three forms share many similarities and are undoubtedly closely related; however, the Turtle Bay form is clearly a distinct species. *Monoceratina* sp. B of Keij

(1953) is also similar to the new species but lacks several details in ornamentation. The apparently Recent species of Keij occurs in redeposited faunas at 847 and 1,947 fathoms in the Celebes Sea, Netherlands East Indies. The genera *Monoceratina* and *Bythoceratina* have not been previously reported from the west coast of America.

Bythoceratina monstruosa, and its North American allies, differ from the New Zealand species of *Bythoceratina* (Hornibrook, 1952: 62–63) in having a smooth median element and knobby alae, lacking a hollow ventrolateral spine. However, one New Zealand species, *B. utilazea* Hornibrook, 1952, from the Lower Miocene to Recent of New Zealand, has close affinity to the present species. These two resemble several Upper Cretaceous *Monoceratina* from South Limburg in the Netherlands, viz., *M. parva, M. pygmaea, M. sulcata, M. pulchra,* and to a lesser degree *M. pseudosulcata,* all of van Veen, 1936. This group is characterized by a dorsally lanceolate shape and the lack of a ventral spine. The species is named for its grotesque ornamentation.

Family CYTHERURIDAE Müller, 1894
Genus *Paracytheridea* Müller, 1894

Paracytheridea sp.
Figs. 13 *a–b*

DIMENSIONS: Specimen USNM 648743 (left valve) T-12: length, 0.31; width, 0.15; height, 0.14.

DISTRIBUTION: As fossils from T-12 (2 valves).

DISCUSSION: Poor preservation and lack of material do not warrant a detailed treatment of the present species. It is possible that the figured specimen, the larger of the two, is a young one, although some species of this genus are not much larger (Morkhoven, 1963:378).

Family HEMICYTHERIDAE Puri, 1953
Genus *Hemicythere* Sars, 1925

Hemicythere obesa n. sp.
Figs. 14 *a–d*

DIAGNOSIS: Large smooth inflated carapace; straight subparallel ventral and dorsal margins;
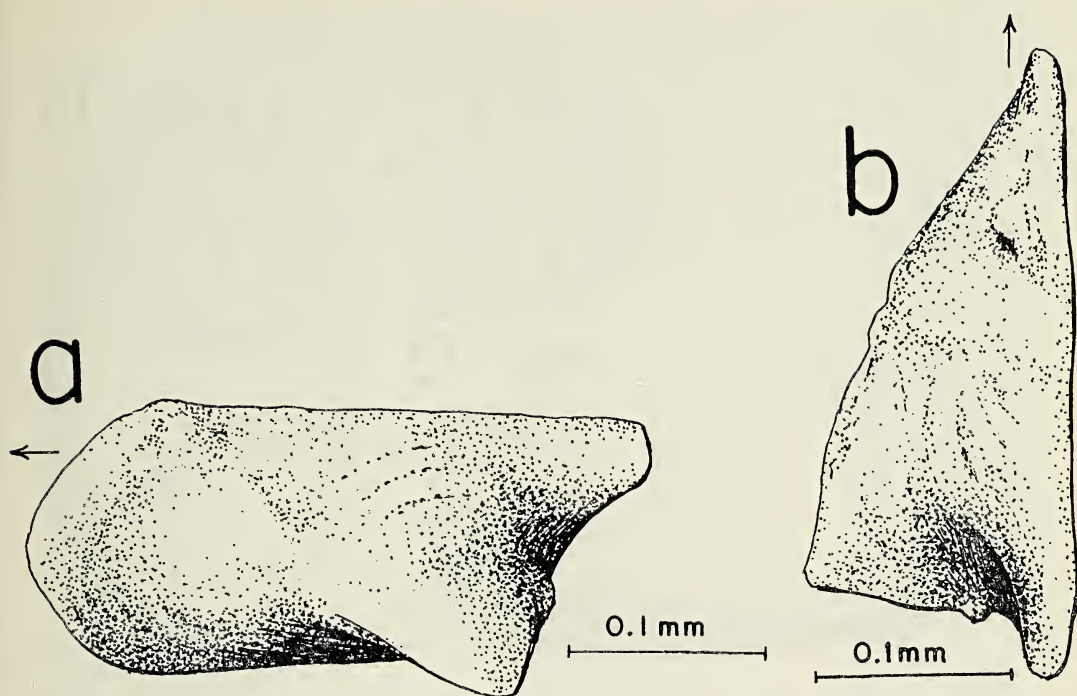
FIG. 13. *Paracytheridea* sp. *a–b,* Specimen USNM 648743; *a,* lateral view of left valve; *b,* dorsal view.

wide faint sulcus, modified holamphidont hinge; adductor muscle scar pattern of at least six scars.

DESCRIPTION: Carapace very inflated, widely but faintly sulcate; dorsal margin straight, subparallel to almost straight ventral margin, both slightly converging posteriorly; short posterodorsal margin straight in left valve, concave in right valve; posteroventral margin rounded, extended, with five or six denticulations; anterior margin broadly rounded, flattened dorsally, finely denticulate in ventral part; left valve overlapping right valve along posterodorsum, at anterodorsal angle, and at ventral inturned area; surface of carapace mostly smooth, sparsely covered with faint pits; narrow ventral ridges continuing partially up anterolateral surface.

Hinge modified holamphidont: anterior tooth of right valve small, with subjacent entire socket; median bar smooth; posterior element elongate, notched twice below.

Adductor muscle scar pattern basically six smaller scars on posterior side of small pit: top scar elongate, or crescent shaped, five circular scars below; antennal scar pattern a triangle of three equal scars on anterior side of pit; two

elongate mandibular scars below antennal group, four or more above adductor group. Radial pore canals straight, simple, apparently very dense (not illustrated); no vestibules present; heavy selvage in left valve with corresponding continuous groove in right valve. Interior heavily pitted.

DIMENSIONS:

SPECIMEN	LENGTH	WIDTH	HEIGHT
Holotype USNM 648744 (entire) T-12	0.83	0.43	0.43
Paratype SDNH 1042 (right valve) T-12	0.83	0.22	0.42
Paratype USNM 648745 (right valve) T-12	0.80	0.22	0.42

DISTRIBUTION: As fossils from T-11 (1 valve) and T-12 (9 valves; 2 entire).

DISCUSSION: The 12 specimens available are poorly preserved and details of the marginal areas are only barely visible using clearing oil and transmitted light. Figure 14 *c* shows only a few of the almost obliterated, apparently abundant radial pore canals. The large marginal pits are exterior, not interior, as might be suggested in the figure.
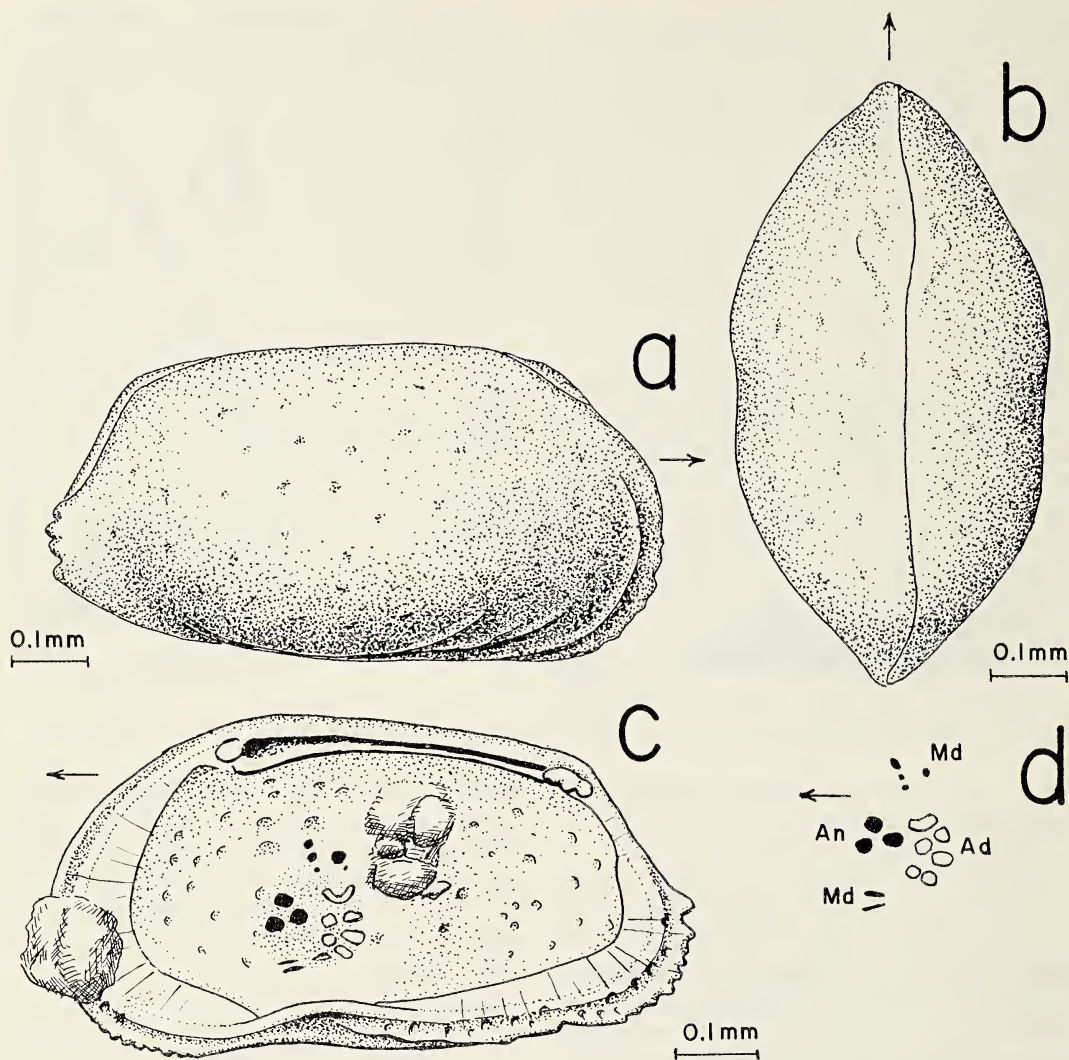
FIG. 14. *Hemicythere obesa* n. sp. *a–b*, Holotype USNM 648744; *a*, side view of entire carapace; *b*, dorsal view of entire carapace; *c*, Paratype SDNH 1042; internal view of right valve; adductor scars in white. *d*, Paratype USNM 648745; muscle scar pattern of right valve; adductor scars in white.

The hinge differs from the typical *Hemicythere* amphidont type by being deeply notched beneath the posterior tooth. The species is named with reference to its highly inflated carapace.

Hemicythere sp.
    Figs. 15 *a–c*

DESCRIPTION: In lateral view: carapace suboval, dorsal margin straight, slightly converging posteriorly with straight ventral margin; anterior and posterior margins broadly rounded, dorsal part of anterior margin more flattened than ventral part, caudal process absent. Ornamentation distinctive; entire surface covered by distinctly flat-topped ridges continuous in centrolateral parts of carapace and discontinuous near margins of carapace; well-defined concentric pattern centered around area coinciding with internal adductor-antennal muscle scar area; eye tubercles low, indistinct, but well-developed internal ocular sinuses are present.
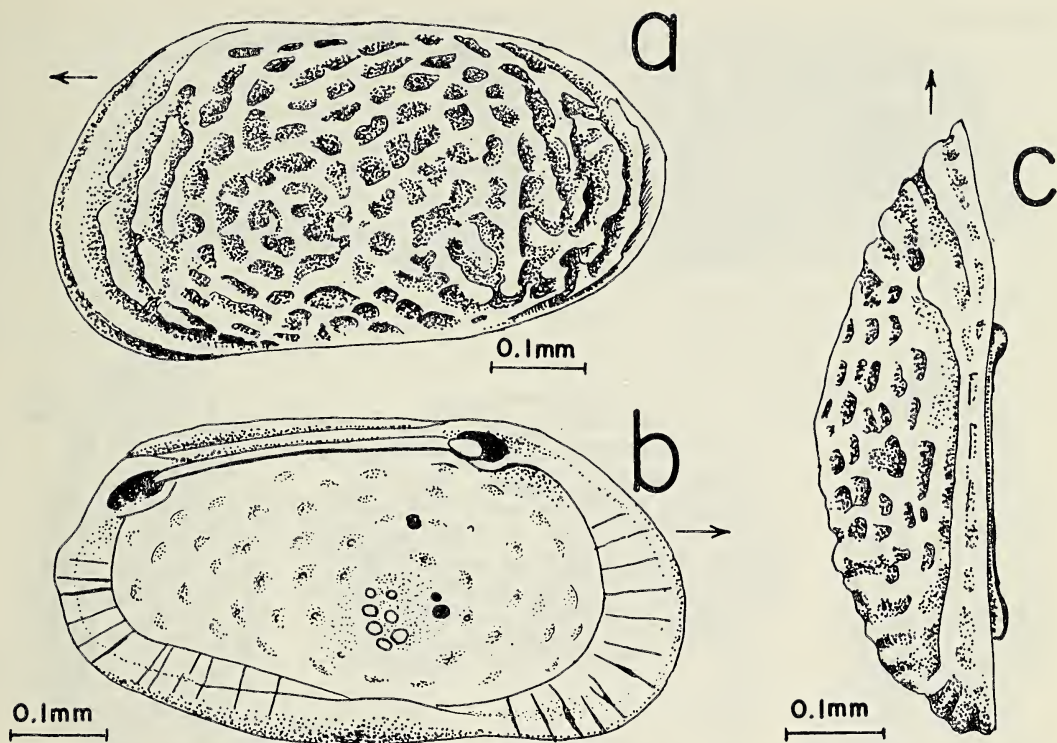
FIG. 15. *Hemicythere* sp. a–c, Specimen USNM 648746; a, external side view of left valve; b, internal view; adductor scars in white; c, dorsal view.

Hinge modified holamphidont: posterior element trilobed; anterior element an entire tooth; median bar smooth, with smooth, somewhat subdued anterior tooth, posterior part of bar projecting (in dorsal view).

Adductor muscle scar pattern distinctive: curved, near-vertical row of four rounded scars on side of shallow depression; top, bottom, and one of middle scars divided into two distinct scars respectively; two antennal scars on anterior side of depression; single (?) weak dorsal mandibular scar present. Radial pore canals moderately abundant, straight, few in antero-ovener with midswellings; normal pore canals numerous, causing deep internal depressions, pores not coinciding necessarily with external lows (some extend through the heavy ornamentation). Moderate selvage present in left valve.

DIMENSIONS: Specimen USNM 648746 (left valve) T-12: length, 0.65; height, 0.35; width, 0.20.

DISTRIBUTION: As fossils from T-1 (1 valve), T-11 (1 entire), and T-12 (1 valve).

DISCUSSION: *Hemicythere* sp. is in many ways comparable to *H. obesa*. An inflated carapace with large internal pits, ventrally notched posterior hinge element, and general shape are common to both species. *H.* sp., however, is smaller, coarsely ornamented, and has a different muscle scar pattern than *H. obesa*. Here, as in the latter species, *H.* sp. disagrees with the generic concept by having an almost hemi-amphidont hinge and an atypically divided adductor muscle scar pattern.

Genus *Mutilus* Neviani, 1928

Mutilus (*Mutilus*) *oahuensis* n. sp.
Figs. 16 a–b

DIAGNOSIS: Conspicuous left valve overreach; combined ornamentation of large reticulations; pronounced bladelike marginal and lateral ridges.
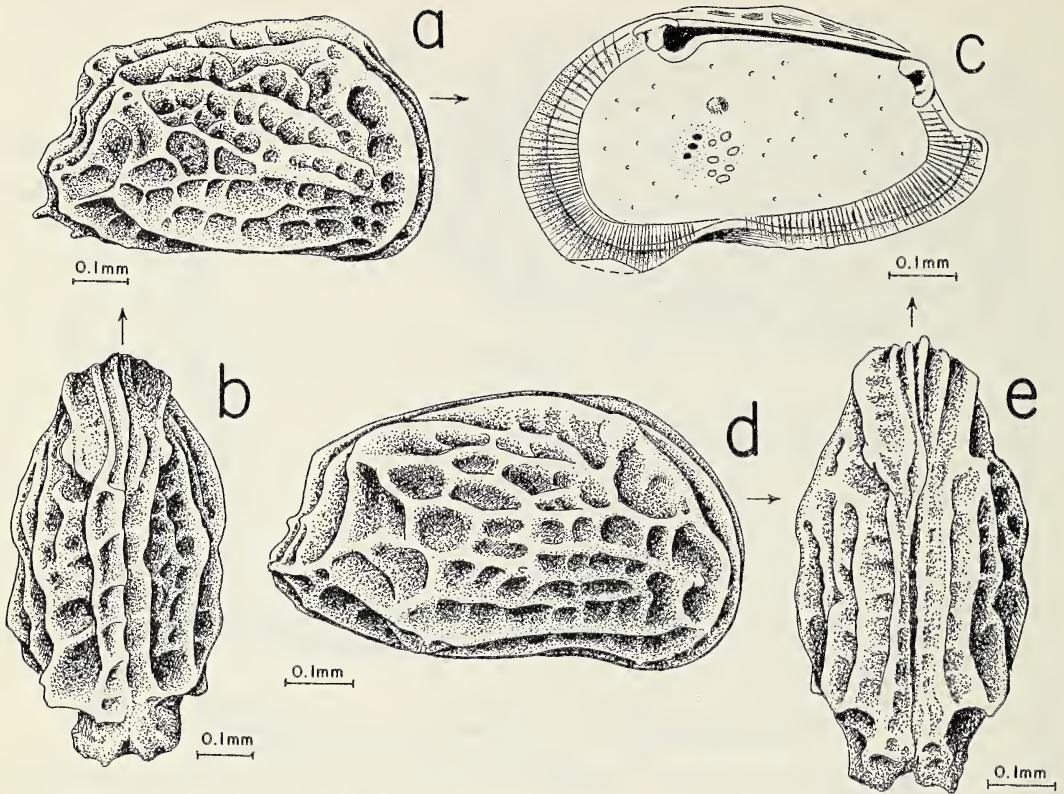
FIG. 16. *Mutilus* (*Mutilus*) *oahuensis* n. sp. *a–b*, Holotype USNM 648751; *a*, right valve view of entire carapace showing dorsally overreaching left valve; *b*, dorsal view. *Mutilus* (*Mutilus*) *palosensis* (Le Roy), 1943. *c*, Plesiotype USNM 648748; internal view of right valve; adductor scars in white. *d–e*, Plesiotype USNM 648747; *d*, right valve view of entire carapace showing slight overreach of left valve; *e*, dorsal view.

DESCRIPTION: In lateral view: anterior margin blunt, somewhat flattened in dorsal part, more tightly rounded in ventral part; ventral margin slightly concave; dorsal margin gently convex in both valves; posterior margin concave above distinct low caudal process. Left valve considerably overreaching but not strongly overlapping right valve dorsally; ornamentation distinctive; surface covered by large deep reticulations bordered by high massive bladelike ridges; marginal ridges same; dorsal ridge turning abruptly anteroventrally at posterodorsal angle, forming high oblique lateral ridge; ventrolateral ridge also prominent. Eye tubercle below anterodorsal angle indistinct, located at juncture of dorsal and anterior marginal ridges and sinuous vertical ridge. Internal features not observed.

DIMENSIONS:

SPECIMEN	LENGTH	WIDTH	HEIGHT
Holotype USNM 648751 (entire) AR	0.75	0.39	0.47
Paratype USNM 648752 (entire) AR	0.72	0.43	0.46
Paratype USNM 648753 (entire) AR	0.75	0.36	0.45
Paratype SDNH 1043 (entire) AR	0.70	0.35	0.41
Paratype SDNH 1044 (entire) AR	0.74	0.37	0.46

DISTRIBUTION: As fossils from AR (1 valve; 7 entire).

DISCUSSION: The internal features of this species are not preserved; however, a Recent species, *Mutilus palosensis* (LeRoy), 1943, from Alijos Rocks, Mexico, most certainly a

closely related form, has typical hemicytherid internal features. Specimens from Alijos Rocks are illustrated for comparative purposes (Figs. 16 *c–e*). Though very similar in general shape and ornamentation, the Hawaiian fossil species is shorter, the larger left valve is relatively higher than the right valve, and the dorsum is straight. Also, the reticulations in the fossil form are deeper and the ridges more bladelike than in *M. palosensis.*

Mutilus(?) coalescens n. sp.
Figs. 17 *a–d*

DIAGNOSIS: Ornamentated with coalescing heavy knobs and poorly defined ridges; highly inflated, subquadrate carapace.

DESCRIPTION: Carapace tumid, as wide as high or wider; left valve slightly larger, overlapping right valve at terminal hinge elements and ventral inturned area. In lateral view: dorsal margin straight to slightly convex; anterior and posterior margins subtruncate, anterior margin sloping down about 60° from the horizontal from sharp anterodorsal angle; posterior margin straight, sloping down about 75° from sharp posterodorsal angle to inconspicuous low caudal process; ventral margin straight to slightly concave, terminating at caudal process.
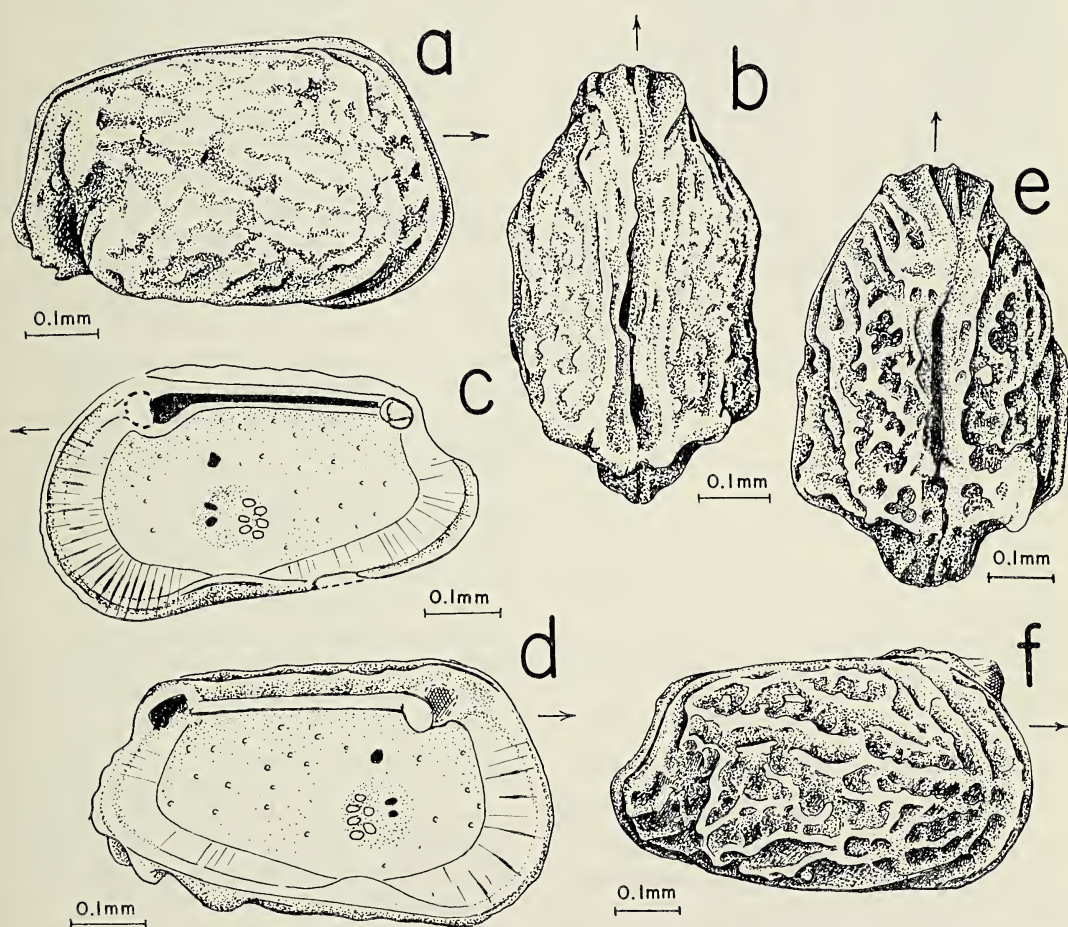
FIG. 17. *Mutilus* (?) *coalescens* n. sp. *a–b,* Holotype USNM 648762, right valve view of entire female (?) carapace; *b,* dorsal view. *c,* Paratype USNM 648763; internal view of female (?) right valve; abductor scars in white. *d,* Paratype SDNH 1045; internal view of male (?) left valve; adductor scars in white. *e,* Paratype USNM 648764; dorsal view of entire female (?) showing deep dorsal groove. *f,* Paratype SDNH 1046; right valve view of entire male (?) showing slight overlap of left valve.

In dorsal view: carapace inflated, greatest width at subcentral swelling and posteroventral extension; broad inconspicuous central sulcus present; caudal process relatively compressed; anterior blunt, with two smooth marginal ridges per valve, converging at anterodorsal angle. Ornamentation heavy, complex, distinctive, of distinct or coalescing heavy knobs and ill-defined ridges with general horizontal trend, adjacent depressions partially filled with secondary (?) growth; marginal ridge of ventral inflation extending around anterolateral surface to well-defined eye tubercle, paralleling outer anterior marginal ridge.

Hingement essentially holamphidont: terminal teeth of right valve entire (posterior tooth faintly trilobed); median bar of left valve heavy, smooth anterior tooth entire.

Adductor muscle scar pattern four in a row on side of deep pit, second and bottom scars divided into two scars; two antennal scars, one above the other, deep within pit; single mandibular scar just dorsal to pit. Radial pore canals very abundant, straight, single, many in anterior with midswellings; no vestibules present; normal pore canals large, sparse; flange in left valve and flange groove in right valve heavy, well developed.

DIMENSIONS:

SPECIMEN	LENGTH	WIDTH	HEIGHT
Holotype USNM 648762 (entire ♀ ?) S-23	0.64	0.37	0.39
Paratype SDNH 1045 (right valve ♀ ?) S-23	0.63	0.18	0.39
Paratype USNM 648763 (left valve ♂ ?) S-23	0.67	0.19	0.40
Paratype USNM 678764 (entire ♀ ?) AR	0.65	0.41	0.37
Paratype SDNH 1046 (entire ♂ ?) AR	0.67	0.44	0.40

DISTRIBUTION: As fossils from S-23 (4 valves; 1 entire) AR (2 valves; 2 entire).

DISCUSSION: Aspects of shape, ornamentation, and musculature of this species are not typical of others in the genus; for this reason the generic assignment is questioned. Two forms occur in the collection, differing only in the degree of development of ornamentation. Specimens illustrated in Figures 17 a–d from station S-23 possess relatively heavier ridges than

those in Figures 17 e–f from station AR. These differences are not considered to be of specific importance, however.

Brady's species of Cythere fungoides (1880: pl. 19, fig. 7) is similar in shape to Mutilus(?) coalescens although they differ in ornament. Unfortunately, the internal features of C. fungoides are unknown and the relationship between these two forms is obscure.

Genus *Jugosocythereis* Puri, 1957

Jugosocythereis venulosus n. sp.

Figs. 18 a–c

DIAGNOSIS: Carapace short, inflated; ornamentation of small reticulations aligned in stripes; subcentral tubercle pitted (without the ridges which are typical of the genus).

DESCRIPTION: In lateral view: dorsal margin straight to slightly convex with small central hump; ventral margin straight, curving upward abruptly at posterior, ending at weak, pointed caudal process; posterodorsal margin weakly concaved above caudal process; anterior margin blunt, smooth, evenly rounded. In dorsal view: carapace tumid, about as wide as high; equally wide at subcentral and posteriorly directed posteroventral tubercles; prominent posterodorsal tubercle present; margins smooth save for some inconspicuous wide spines in posteroventer; left valve larger and strongly overlapping right valve above terminal hinge elements; ornamentation unique: deep pits coalescing into narrow horizontally trending furrows, giving shell a striped appearance; eye tubercle broad, deep-set, with postjacent prominent pit.

Adductor muscle scar pattern partially obscured; one of middle scars divided; two antennal scars on anterior side of pit, large mandibular scars above subcentral pit, double mandibular scar below pit. Anterior and posterior vestibules narrow; radial pore canals obscure, apparently straight and simple, with some midswellings; normal pores small, sparse. Hingement probably hol- or hemiamphidont.

DIMENSIONS:

SPECIMEN	LENGTH	WIDTH	HEIGHT
Holotype USNM 678765 (entire) T-12	0.61	0.36	0.39
Paratype SDNH 1047 (right valve) T-12	0.62	0.17	0.36
Paratype USNM 648766 (entire) T-12	0.61	0.35	0.36
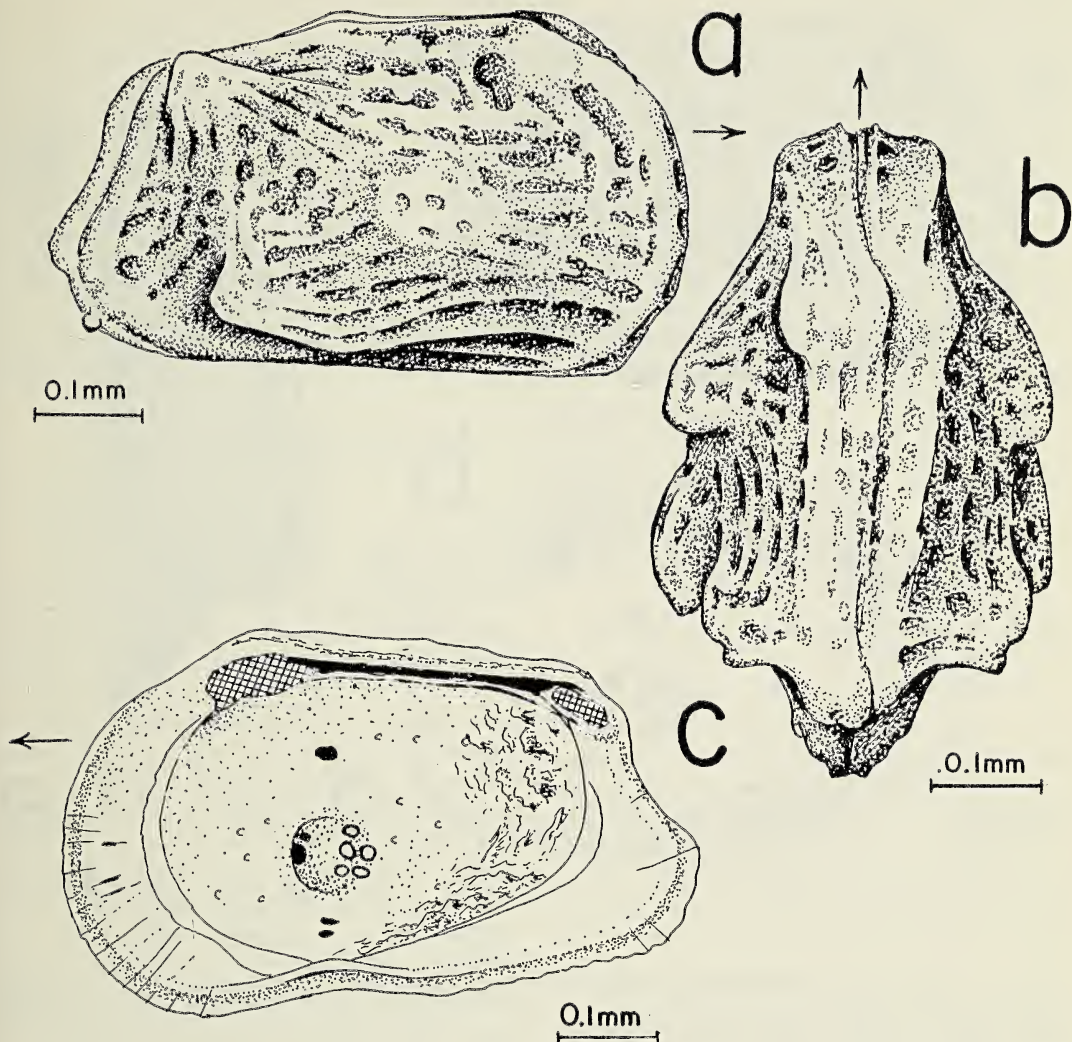
FIG. 18. *Jugosocythereis venulosus* n. sp. *a–b,* Holotype USNM 648765; *a,* lateral right valve view of carapace showing overlap of left valve; *b,* dorsal view. *c,* Paratype SDNH 1047; internal view of poorly preserved right valve; adductor scars in white.

DISTRIBUTION: As fossils from T-11 (1 entire) and T-12 (5 valves; 3 entire).

DISCUSSION: This species represents an extreme form of ornamentation for *Jugosocythereis*. The surface is finely reticulate and practically without the characteristic small ridges. Also, the subcentral swelling, alae, and posterodorsal complex are extremely tuberculate and localized. Sexual dimorphism in the species is not apparent. The species is named for its veinlike ornamentation.

Genus *Quadracythere* Hornibrook, 1952

Quardracythere hornibrooki n. sp.
Figs. 19 *a–e*

DIAGNOSIS: Smooth median bar; trilobed posterior tooth; smooth anterior margin; divided adductor muscle scar pattern.

DESCRIPTION: Carapace stout, inflated, subquadrate. In lateral view: slightly concave dorsal margin symmetric with convex ventral margin; posterior margin concave in upper part, forming low caudal process in lower part; poorly devel-
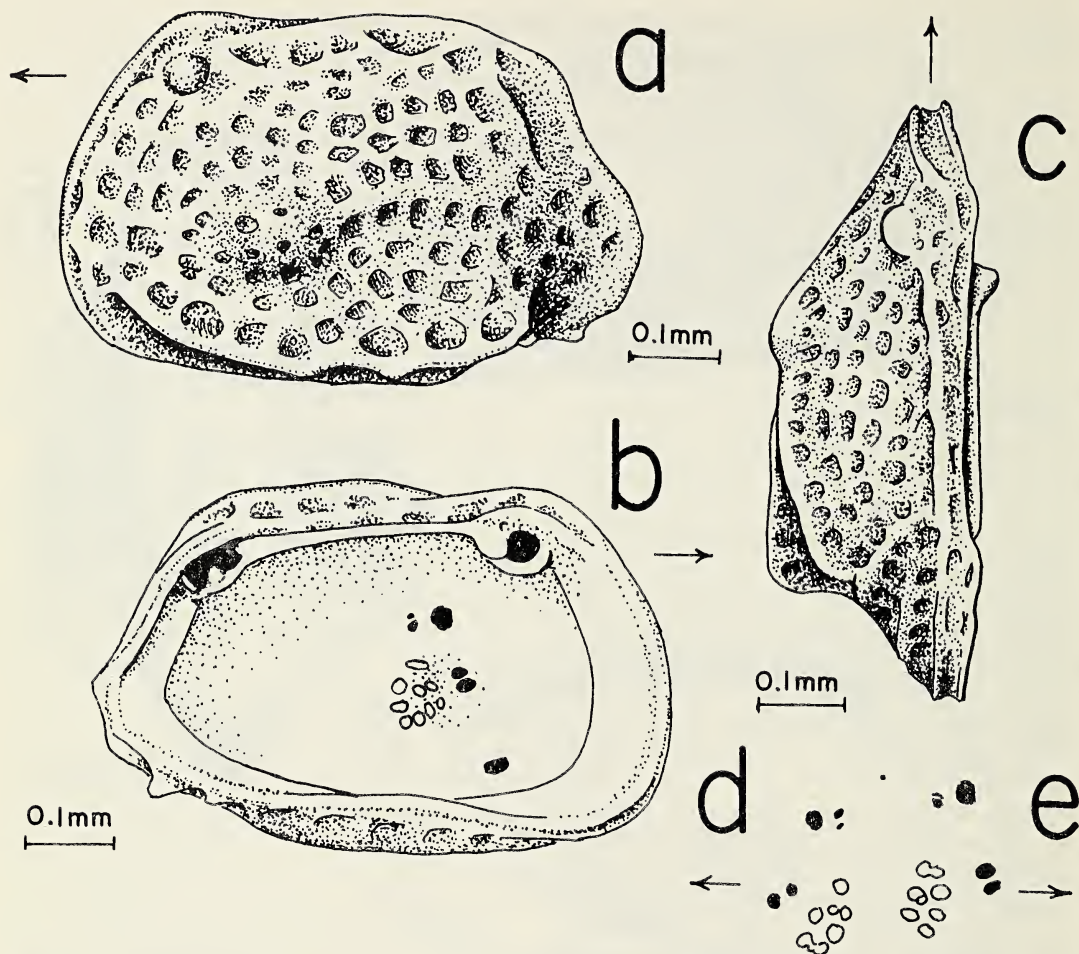
FIG. 19. *Quadracythere hornibrooki* n. sp. *a–c,* Holotype USNM 648758; *a,* lateral view of left valve; *b,* internal view; adductor scars in white; *c,* dorsal view. *d,* Paratype USNM 648760; muscle scar pattern of right valve. *e,* Paratype USNM 648761; muscle scar pattern of left valve; adductor scars in white.

oped narrow ridge from eye tubercle along dorsum turning down in posterodorsal area forming sinuous median ridge terminating at subtle subcentral tubercle; prominent ventral ridge posteriorly extended forming weak alae; surface with large, deep various-sized reticulations.

Dentition holamphidont: median element of left valve a smooth bar with stubby anterior tooth, bar thickening posteriorly; posterior tooth of right valve entire, reniform; posterior socket of left valve with small ventral and posterior teeth.

Adductor muscle scar pattern complex; top scar entire, second scar down divided into two or three scars, bottom two scars variously divided into 3–5 smaller scars. Two antennal scars

located anterior to upper adductor scars, large dorsal mandibular scar present. Normal pores of sieve type, large, forming deep pits internally.

DIMENSIONS: See Table 6.

DISTRIBUTION: As fossils from T-2 (1 valve), T-11 (1 valve), and T-12 (26 valves; 2 entire).

DISCUSSION: Generic discrepancies in dentition and musculature exist between species of typical *Quadracythere* from New Zealand and the present species. In the latter, the median bar is smooth, not crenulate, and the adductor scar pattern is usually divided.

The Hawaiian individuals are somewhat comparable to *Quadracythere mediaruga* Hornibrook (Kaiatan-Recent, New Zealand) in shape and placement of ridges, but lack the antero-

TABLE 6

DIMENSIONS OF *Quadracythere hornibrooki* N. SP.

SPECIMEN	LENGTH	WIDTH	HEIGHT
Holotype USNM 648758 (left valve) T-12	0.77	0.21	0.50
Paratype USNM 648759 (left valve) T-12	0.75	0.22	0.50
Paratype SDNH 1048 (right valve) T-12	0.80	0.22	0.52
Paratype SDNH 1049 (left valve) T-12	0.80	0.25	0.50
Paratype USNM 648760 (right valve, young) T-12	0.69	0.18	. . .
Paratype USNM 648761 (left valve) T-12	0.77	0.26	0.52

marginal denticulations and are more ovate in lateral outline.

Genus *Loxoconcha* Sars, 1866

Loxoconcha batei n. sp.
Figs. 20 *a–b*

DIAGNOSIS: Straight dorsal margin; evenly inflated carapace; extremely complicated ornamentation of high, flat-topped discontinuous ridges surrounded by less pronounced network of reticulations.

DESCRIPTION: In lateral view: carapace oblong; dorsal margin straight; ventral margin gently convex, curving upward posteriorly forming subtle arcuate posteroventral ridge; anterior margin usually broadly rounded; posterior margin straight, sloping upward 60° in ventral half; ornamentation distinctive: heavy discontinuous flat-topped ridges and flat-topped spines rising high above a coarsely reticulate lower surface; large low eye tubercles present. Carapace evenly inflated in dorsal view.

Hinge gongylodont: left valve anterior element a short rounded tooth, postadjacent socket and smaller tooth; median element a crenulate bar; posterior element a very small socket, round postadjacent tooth, and larger socket, sockets interconnected. Well-developed accommodation groove present above median element of left valve.

Adductor muscle scar pattern an arcuate row of four smaller quadrate scars on slight median ridge (not expressed as an external sulcus), lowest scar in front of top three scars; quadrate antennal scar in front of top two adductor scars; radial pore canals not observed; no vestibules present; heavy continuous selvage along duplicature of left valve with corresponding heavy groove in right valve.

DIMENSIONS:

SPECIMEN	LENGTH	WIDTH	HEIGHT
Holotype USNM 648771 (left valve ♂) T-12	0.58	0.20	0.35
Paratype SDNH 1050 (right valve ♂) T-12	0.58	0.18	0.33
Paratype SDNH 1051 (left valve ♀) T-12	0.53	0.20	0.34
Paratype USNM 648772 (left valve ♂) T-12	0.59	0.20	0.36

DISTRIBUTION: As fossils from T-1 (1 valve), T-7 (1 valve), T-11 (3 valves), T-12 (16 valves; 1 entire), and S-23 (1 valve).

DISCUSSION: The ornamentation of this species is very distinctive. The high ridges show no organized pattern but are flat-topped and widest on top, forming a distinct upper surface above and apart from the lower reticulations.

The species is named in honor of Dr. R. H. Bate of the British Museum (Natural History).

Loxoconcha condyla n. sp.
Figs. 21 *a–b*

DIAGNOSIS: Straight dorsal margin; ornamented with small poorly defined reticulations; compressed postroventral margin beneath a high caudal process; weak pointed posterodorsal tubercle.

DESCRIPTION: In lateral view: carapace elongate, length about twice the height; dorsal margin straight, anterior margin somewhat obliquely rounded; ventral margin beneath high caudal process constricted into posteroventral keel. In dorsal view: carapace sublenticular, compressed behind poorly developed dorsal tubercles near posterior; greatest width central at broad subcentral swelling. Ornamentation of poorly defined small reticulations (or large pits); anteromarginal ridge grooved by row of small pits; eye tubercles well developed.
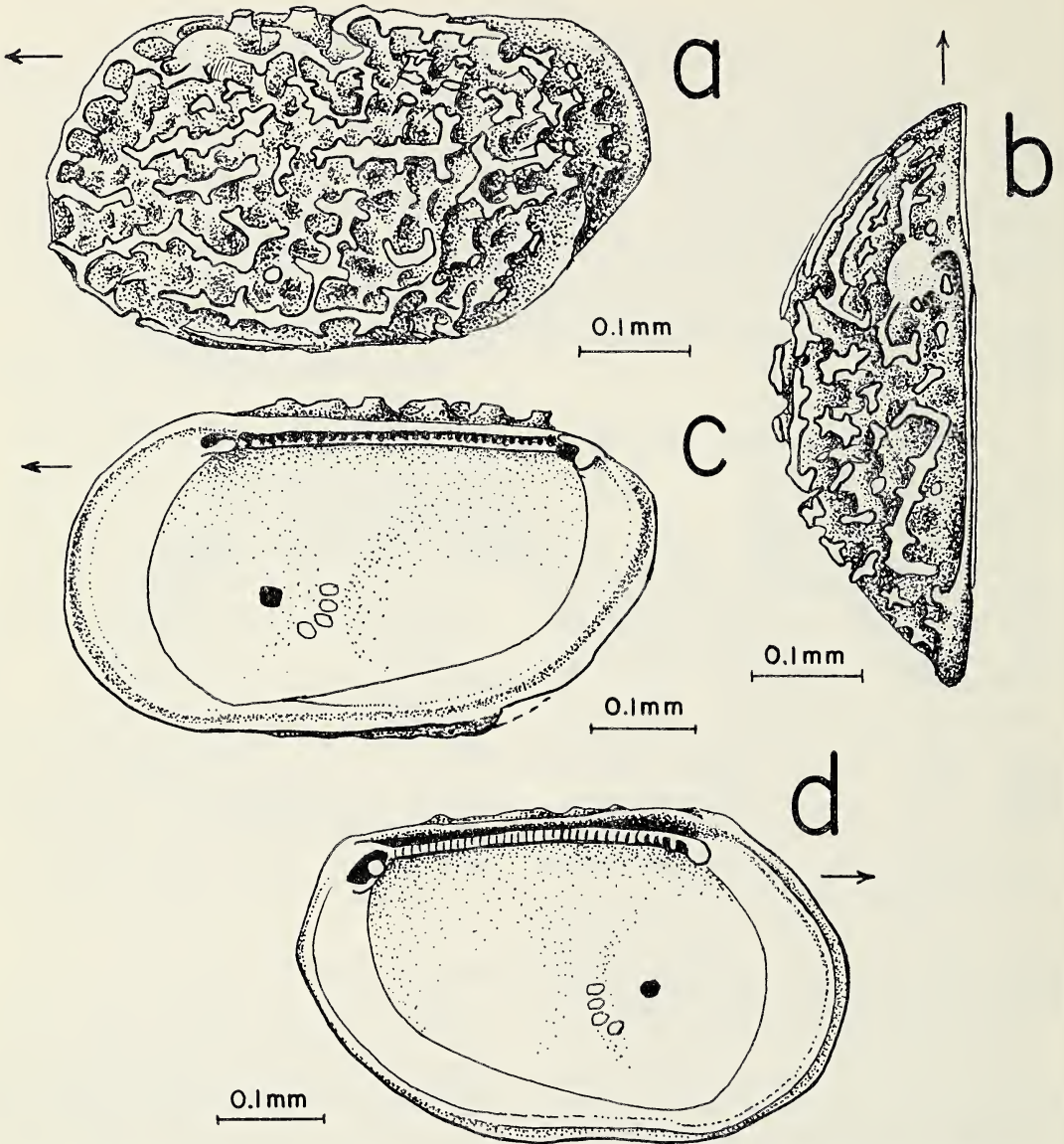
FIG. 20. *Loxoconcha batei* n. sp. *a–b,* Holotype USNM 648771; *a,* lateral view of male left valve; *b,* dorsal view. *c,* Paratype SDNH 1050; internal view of male right valve; adductor scars in white; marginal features not preserved. *d,* Paratype SDNH 1051, internal view of female left valve; adductor scars in white; marginal features not preserved.

Duplicature of moderate width; radial pores sparse, straight, simple; vestibules absent; normal pores somewhat abundant, of intermediate size, apparently corresponding with external pits. Adductor muscle scar pattern of four small scars in short vertical row, third from top scar divided; two antennal scars in front of adductor group.

DIMENSIONS:

SPECIMEN	LENGTH	WIDTH	HEIGHT
Holotype USNM 648773 (entire) T-12	0.51	0.24	0.29
Paratype USNM 648774 (left valve) T-12	0.48	0.13	0.29

DISTRIBUTION: As fossils from T-12 (7 valves), and S-23 (1 entire); Recent from HA
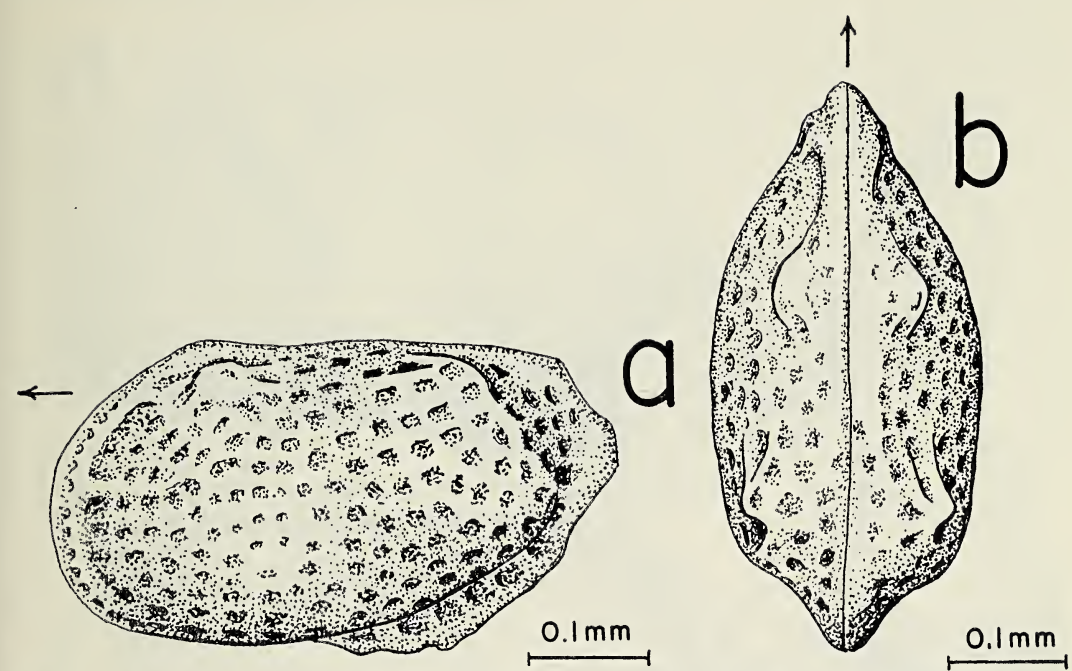
FIG. 21. *Loxoconcha condyla* n. sp. *a–b*, Holotype USNM 648773; *a*, lateral left valve view of entire carapace; *b*, dorsal view.

(6 valves; 5 entire); T-13 (2 valves; 1 entire).

DISCUSSION: *Loxoconcha postdorsolata* Puri, 1960 from the Gulf of Mexico and *Loxoconcha condyla* are similar. The latter does not have the large posterodorsal tubercle that the former has; it does, however, possess a small pointed extension of the carapace in the same area.

Recent representatives of the species occur in the Hawaiian Islands at 22 fathoms on Penguin Bank and at 5 fathoms in Hanauma Bay. At both Recent stations specimens are much smaller than the fossils, i.e., only 0.44 mm in length. In all other aspects the Recent forms appear conspecific with the fossil forms. The description of the internal features was taken from these better preserved specimens.

The species is named with reference to the small, knuckle-like enlargement in the posterodorsum. This feature is variably developed, being practically absent in some individuals.

Loxoconcha sp.
    Figs. 22 *a–b*

DESCRIPTION: In lateral view: shell subrhomboidal; length twice the height; dorsum straight in anterior half, undulatory in posterior half, parallel with straight ventral margin; anterior margin bluntly rounded; posterior margin bluntly pointed in dorsal half; ornamentation of faint random pustules. In dorsal view: shell conspicuously sulcate toward posterior; anterior pointed; posterior blunt.

Hinge gongylodont: posterior element of right valve a socket bracketed by two teeth connected above; anterior element a tooth bracketed by two sockets; other internal features obscured.

DIMENSIONS: Specimen USNM 648775 (right valve) T-12: length, 0.52; width, 0.13; height, 0.28.

DISTRIBUTION: As fossil from T-12 (1 entire).

DISCUSSION: Lack of adequate specimens prohibits a more detailed description of the species. The single right valve is unquestionably fossil, as attested by the partial encrustation of manganese oxide on its outer surface (Fig. 22 *b*).

To the writer's knowledge there are no known pustulose species in the genus *Loxoconcha*. The pustules on the present species are probably a secondary effect caused by corrosion, the sieve pores being somehow more resistant than the remainder of the valve.
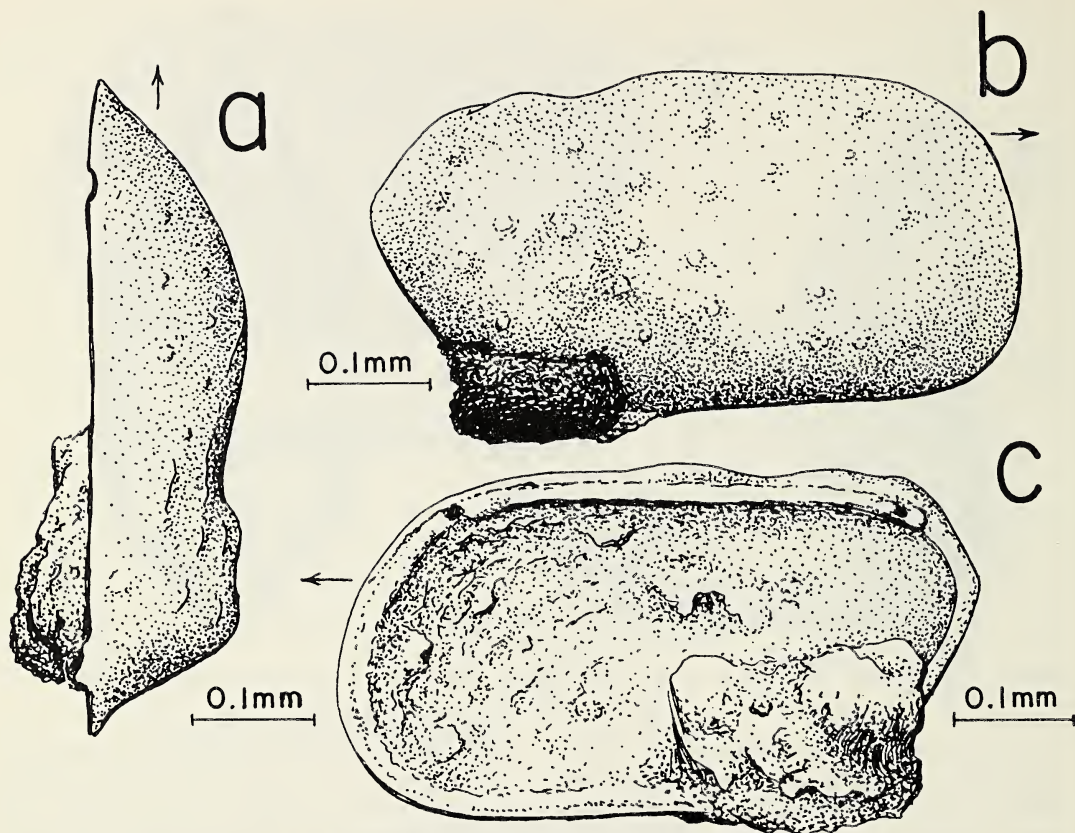
FIG. 22. *Loxoconcha* sp. *a–c,* Specimen USNM 648775; *a,* dorsal view of right valve showing postero-lateral sulcus; *b,* lateral view showing pustulose surface, MnO_2 obscuring posteroventral area; *c,* internal view.

Loxoconcha longispina Keij, 1953
Figs. 23 *a–d*

Loxoconcha alata Brady, 1880. Rept. Voyage *Challenger,* Zool. 1, pt. 3, p. 122, pl. 27, figs. 6 *a–j.*

Loxoconcha alata longispina Keij, 1953. Koninkl. Nederl. Akad. van Wetenschappen, Amsterdam, ser. B, vol. 56, pt. 2, p. 160, pl. 1.

DIAGNOSIS: Short rhomboidal carapace; well-developed ventral tubercle; faint central sulcus; pronounced reticulate ornamentation.

DESCRIPTION: In lateral view: carapace short, rhomboidal; dorsal margin straight, parallel to straight ventral margin; anterior margin evenly rounded but flattened in anterodorsum; pointed caudal process in upper half of posterior margin; broad subcentral tubercle and faint post-adjacent median sulcus present; large pointed tuberculate alae ventrally extended; broad postero-dorsal enlargement sometimes developed.

Eye tubercles large; ornamentation of deep reticulations, elongate on ventral knob, small on subcentral tubercle. In dorsal view: carapace much wider than high due to massive posteriorly pointing knobs; posterior laterally compressed.

Hingement gonglyodont: anterior element of right valve a rounded socket with postadjacent round tooth and small socket; sockets connected above tooth; median element a crenulate groove, coarser at ends; posterior element a large projecting reniform tooth; strong accommodation groove above median element of left valve.

Adductor muscle scar pattern a row of four smaller equant scars on side of pit; large single antennal scar anterior to top two adductor scars; large conspicuous mandibular scar dorsal to adductor group on median ridge. Continuous flange and large groove around anterior-ventral-posterior duplicature of right valve; left valve with corresponding well developed selvage.
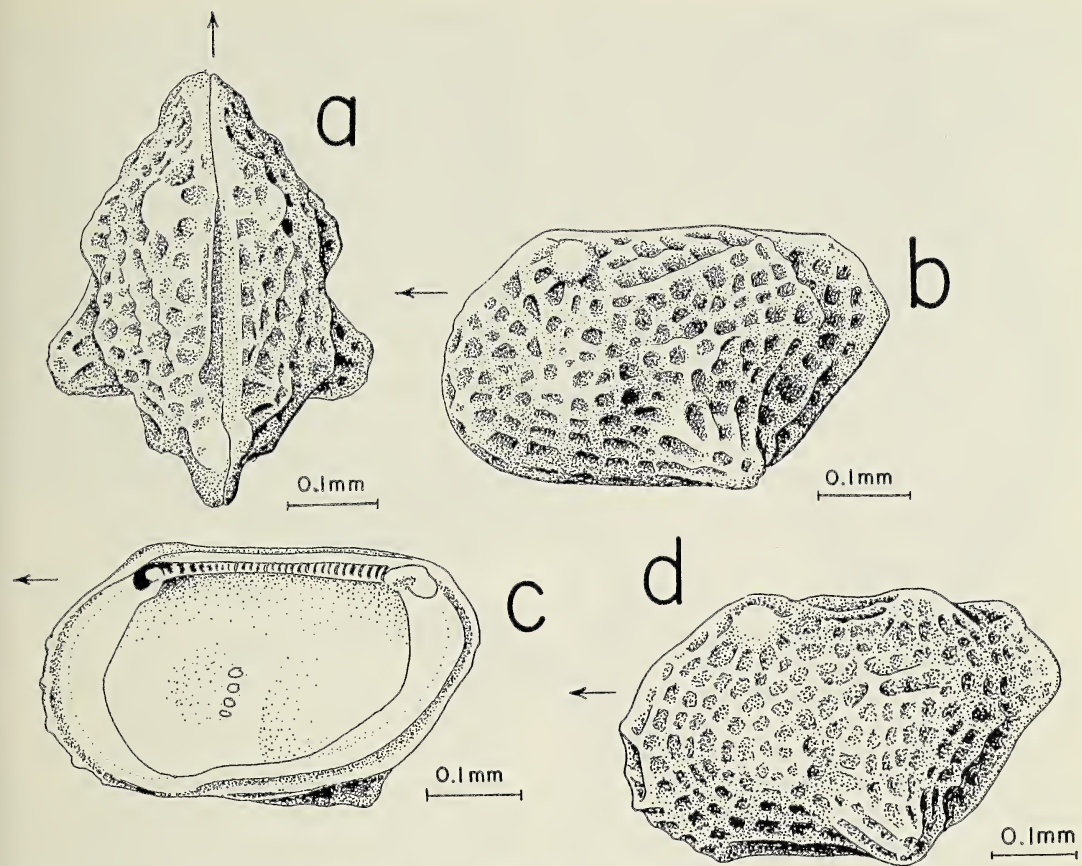
FIG. 23. *Loxoconcha longispina* Keij, 1953. *a–b,* Plesiotype USNM 648776; *a,* dorsal view of entire carapace; *b,* lateral left valve view. *c,* Plesiotype SDNH 1052; internal view of right valve, marginal features not preserved. *d,* Plesiotype USNM 648777; lateral left valve view of dorsally tuberculate form.

DIMENSIONS: See Table 7.

DISTRIBUTION: As fossils from T-1 (2 valves), T-11 (2 valves; 1 entire), and T-12 (105 valves; 6 entire); Recent from the Hawaiian Islands at T-13 (2 valves), Easter Island at EA-1 (3 valves); reported by Brady (1880) off Honolulu at 40 fathoms, and by Brady (1890) from New Caledonia at 3–6 fathoms and Fiji in the littoral zone; reported by Keij (1953) from 364–4483 m (redeposited) in the Banda, Java, and Celebes seas.

DISCUSSION: *Loxoconcha longispina* occurs in great abundance at T-12, but is strangely absent from most other stations from the drowned ter-

TABLE 7

DIMENSIONS OF *Loxoconcha longispina* KEIJ, 1953

SPECIMEN	LENGTH	WIDTH	HEIGHT
Plesiotype USNM 648776 (entire) T-12	0.53	0.38	0.32
Plesiotype USNM 648777 (right valve) T-12	0.54	0.24	0.34
Plesiotype USNM 648778 (right valve) T-12	0.50	0.19	0.30
Plesiotype USNM 648779 (entire) T-12	0.54	0.39	0.32
Plesiotype SDNH 1052 (right valve) T-12	0.51	0.21	0.30
Plesiotype SDNH 1053 (left valve) T-12	0.53	0.21	0.32
Plesiotype SDNH 1054 (right valve) T-12	0.52	0.20	0.32

races. Brady's living specimens of *L. alata* off Honolulu are much smaller (length 0.44 mm) than those dealt with here, and his figures do not show the slight median compression. Adult Recent specimens from T-13, however, are comparable to Brady's form except that they are the same size as the fossil form, i.e., 0.52 mm long. The Recent form has more winglike alae with a more posteriorly pointing trend. Sexual dimorphism with thinner males(?), as noted by Brady, does not occur in the present specimens. Both fossil and Recent forms possess a slight enlargement in the posterodorsum resembling *Loxocorniculum* (Benson and Coleman, 1963); however, this enlargement does not always occur in the fossils.

Some confusion exists between the type species of *Loxoconcha alata* Brady, 1868*b*, from the Mediterranean, and forms similar to the present species. The original description of *L. alata* shows an elongate, finely and concentrically pitted carapace with pointed alae. In dorsal view it is more anteriorly acuminate. Keij's identification of *L. alata* (Keij, 1953: 160) is probably based on Brady's (1880) misidentification, as was Fyan's (1916), even though Brady (1886) expressed doubts about his earlier identification when he stated that the specimens comprising the species *L. alata* Brady, 1880 "are, I think, identical to" *L. gibbera* from Ceylon. They probably are not, and there appear to be several species of alate loxoconchids from the Mediterranean, Indian, and Pacific regions. Other papers reporting, but not describing, "*L. alata* Brady," are by Brady (1886, 1890), Chapman (1902), Scott (1905), and Bold (1946*b*).

Genus *Loxoconchella* Triebel, 1954

Loxoconchella honoluliensis (Brady), 1880
    Figs. 24 *a–c*

Loxoconcha honoluliensis Brady, 1880. Rept. Voyage *Challenger*, Zool. 1, pt. 3, p. 118, pl. 28, figs. 6 *a–f*.

Loxoconchella honoluliensis (G. S. Brady) Triebel, 1954. Senckenbergiana 35, p. 19, pl. 1, figs. 1–6.

DIAGNOSIS: Evenly inflated punctate carapace; prominent posteroventral keel; and lenticular shape in dorsal view.

DESCRIPTION: In lateral view: greatest carapace height in posterior half; dorsal margin straight between high eye tubercle and concave posterodorsum; anterior margin evenly and broadly rounded; ventral margin straight in anterior half; caudal process distinct, at midheight; surface finely punctate (not illustrated). In dorsal view: carapace lenticular; greatest width at midlength; posterior compressed; left valve overlapping right valve in posterior third.

Hinge adont: bar of left valve a continuation of anterior margin along dorsum to posterodorsal cardinal angle, with well-developed centrodorsal accommodation groove; posterior element a distinct groove from posterodorsal cardinal angle to base of caudal process. Other internal features not preserved.

DIMENSIONS:

PLESIOTYPE	LENGTH	HEIGHT	WIDTH
USNM 648780 (entire ♀) T-4	0.67	0.47	0.34
SDNH 1055 (entire ♂) T-13	0.52	0.36	0.25
SDNH 1056 (right valve ♀) T-4	0.65	0.46	0.17

DISTRIBUTION: As fossils from T-1 (2 valves), T-4 (1 valve; 1 entire), and T-7 (6 valves; 2 entire); found living in the Hawaiian Islands at T-13 (1 valve; 1 entire) and Easter Island at EA-1 (2 valves). Reported living by Brady (1880) off reefs at Honolulu at 40 fathoms, and by Brady (1890) at New Caledonia at 2–6 fathoms, and at Fiji and Samoa in the littoral zone.

DISCUSSION: Variation in the development of reticulations occurs in the present specimens, with a few individuals from T-7 being ornamented somewhat like *Loxoconchella anomala*. However, the reticulations on *L. honoluliensis* are never as deep as on *L. anomala*.

Following Brady (1880:117), the compressed form is considered to be the male. This expression of sexual dimorphism is uncommon in the family Loxoconchinae, where the males are usually longer than the females.

Loxoconchella anomala (Brady), 1880
    Figs. 25 *a–f*

Loxoconcha anomala Brady, 1880. Rept. Voyage *Challenger*, Zool. 1, pt. 3, p. 123, pl. 28, figs. 5 *a–d*.
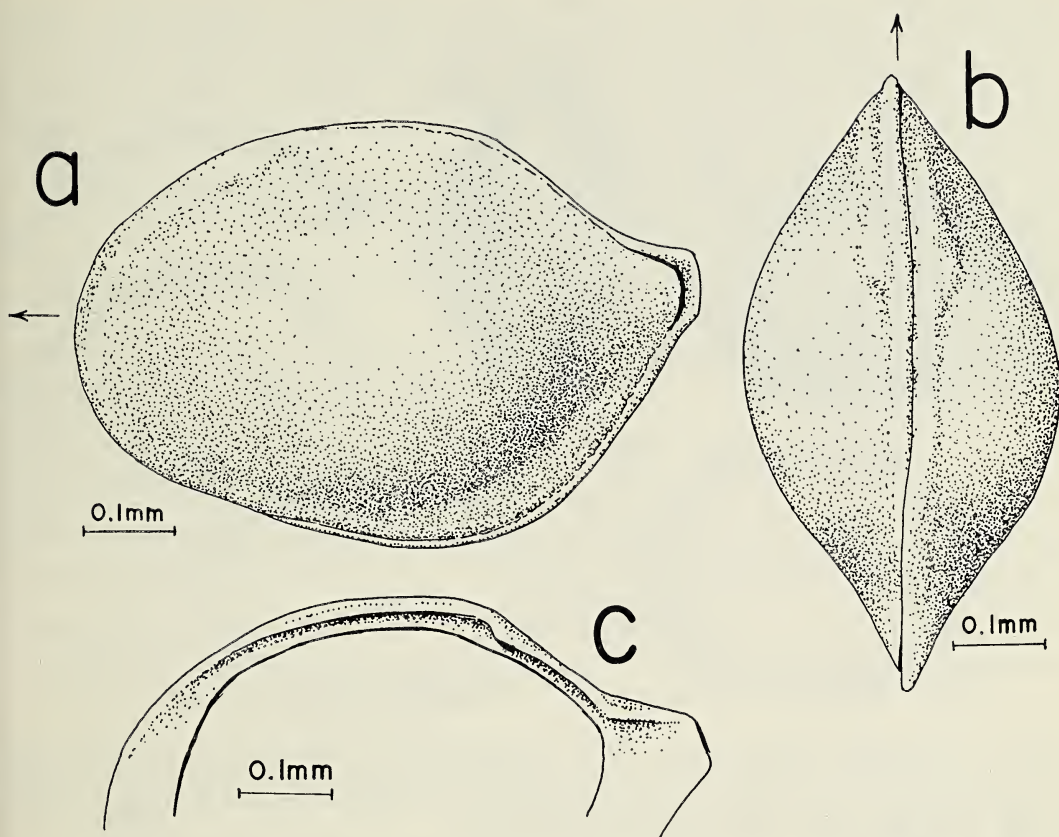
FIG. 24. *Loxoconchella honoluliensis* (Brady), 1880. *a–b,* Plesiotype USNM 648780; *a,* left valve view of slightly deformed entire female carapace; *b,* dorsal view. *c,* Plesiotype SDNH 1056; hinge view of right valve.

DIAGNOSIS: Heavily reticulate, posterodorsally inflated carapace; broad caudal process; relatively simple radial pore canals.

DESCRIPTION: In lateral view: dorsal margin straight from large low-set eye tubercle to highest point just behind carapace midlength, then concave upward to end of high, large caudal process; ventral margin gently and evenly rounded, continuous with evenly rounded anterior margin; posterior margin below caudal process very slightly concave; surface heavily reticulate except on smooth caudal process, reticulations forming concentric pattern; weak marginal ridge from eye tubercle to posteroventer around anterior margin. In dorsal view: carapace diamond shaped, widest just behind center at subtle knoblike posterodorsolateral inflations. Dimorphism of narrow males(?) and wide females(?).

Hinge adont: anterior element of right valve a short groove with ventroadjacent short bar, groove continuous with median element of a straight smooth furrow; posterior element a long straight smooth bar; accommodation groove above median element of left valve. Adductor muscle scar pattern of four small elongate scars in curved row, top scar larger and apart from other three; larger single antennal scar anterior to top adductor scar. Duplicature wide, anterior and posteroventral vestibules present; radial pore canals long, dividing into three near margin, variable, some widened, as elongate extensions of the vestibule; normal pores small, several to each reticulation, interior surface unpitted.

DIMENSIONS: See Table 8.

DISTRIBUTION: As fossils from T-1 (1 valve), T-4 (1 valve; 1 entire), T-7 (2 valves), T-11 (1 valve; 1 entire), and T-12 (19 valves; 4 entire), and S-23 (1 valve). Reported by Brady
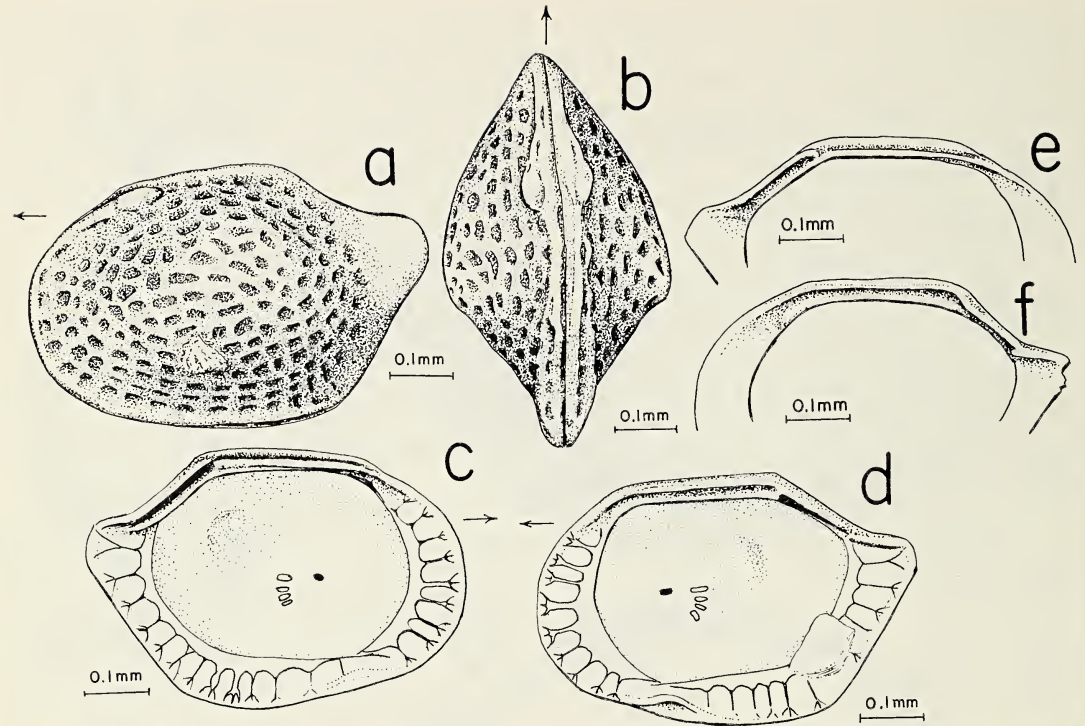
FIG. 25. *Loxoconchella anomala* (Brady), 1880. *a,* Plesiotype USNM 648781; side view of male left valve. *b,* Plesiotype SDNH 1057; dorsal view of entire male carapace. *c,* Plesiotype USNM 648782; internal view of left valve. *d,* Plesiotype SDNH 1058; internal view of right valve. *e,* Plesiotype USNM 648793; hinge view of left valve. *f,* Plesiotype SDNH 1059; hinge view of right valve.

(1880) off reefs at Honolulu, Hawaii at 40 fathoms, and by Brady (1890) at New Caledonia at 3–6 fathoms and Fiji in the littoral zone.

DISCUSSION: *Loxoconchella anomala* differs from the type species, *L. honoluliensis,* by having less complex vestibules and large dorso-lateral inflations, especially well developed in the wider form. Of lesser importance between the two species, *L. anomala* is deeply reticulate

whereas *L. honoluliensis* is punctate to lightly reticulate.

Family PARADOXOSTROMATIDAE
Brady and Norman, 1889
Genus *Paradoxostoma* Fischer, 1855

Paradoxostoma sp. A
Figs. 26 *a–b*

DESCRIPTION: In lateral view: carapace anteriorly acuminate; venter slightly concave;

TABLE 8

DIMENSIONS OF *Loxoconchella anomala* (BRADY), 1880

SPECIMEN	LENGTH	WIDTH	HEIGHT
Plesiotype USNM 648781 (left valve ♂) T-12	0.63	0.19	0.42
Plesiotype USNM 648782 (left valve ♂) T-12	0.59	0.18	0.40
Plesiotype USNM 648783 (entire ♀) T-12	0.63	0.38	0.45
Plesiotype USNM 648793 (left valve ♀) T-12	0.64	0.23	0.45
Plesiotype SDNH 1057 (entire ♂) T-12	0.62	0.33	0.40
Plesiotype SDNH 1058 (right valve ♂) T-12	0.59	0.17	0.40
Plesiotype SDNH 1059 (right valve ♂) T-12	0.60	0.18	0.41

anterior bluntly pointed at midheight; dorsum angled, with posterior and anterior sloping parts; greatest height in posterior half; surface smooth. In dorsal view: carapace compressed; terminally acuminate; greatest width at mid-length.

DIMENSIONS: Specimen USNM 648784 (entire T-12: length, 0.53; width, 0.14; height, 0.25.

DISTRIBUTION: As fossil from T-12 (1 entire).

DISCUSSION. In general shape the present species approaches *Paradoxostoma complanatus* (Brady), 1880, from Kerguelen Island, South Indian Ocean. Both species possess a bluntly pointed caudal process, low height, and small, somewhat pointed anterior margin. But the Hawaiian species is more anteriorly inflated, has a concave venter, and is smaller.

Paradoxostoma sp. B
   Figs. 27 *a–b*

DESCRIPTION: Carapace smooth, elongate. In lateral view: ventral and dorsal margins sub-parallel, converging slightly toward anterior; dorsal margin almost straight, gently convex; ventral margin straight at midlength, curving up posteriorly beneath poorly developed high caudal process, curving up more gradually anteriorly to a blunt anterior margin. In dorsal view: carapace terminally acuminate, greatest width at middle; posterior sharply acuminate; anterior somewhat blunt. Duplicature wide, with greatest width posteroventral.

DIMENSIONS: Specimen USNM 648785 (left valve) T-12: length, 0.69; width, 0.08; height, 0.27.

DISTRIBUTION: As fossil from T-12 (1 valve).

DISCUSSION: The unusually straight dorsum and apparent lack of dentition are not characteristic of the genus *Paradoxostoma*, although the high caudal process and anteriorly narrowing carapace are.

The collection consists of a single left valve in poor condition from station T-12.
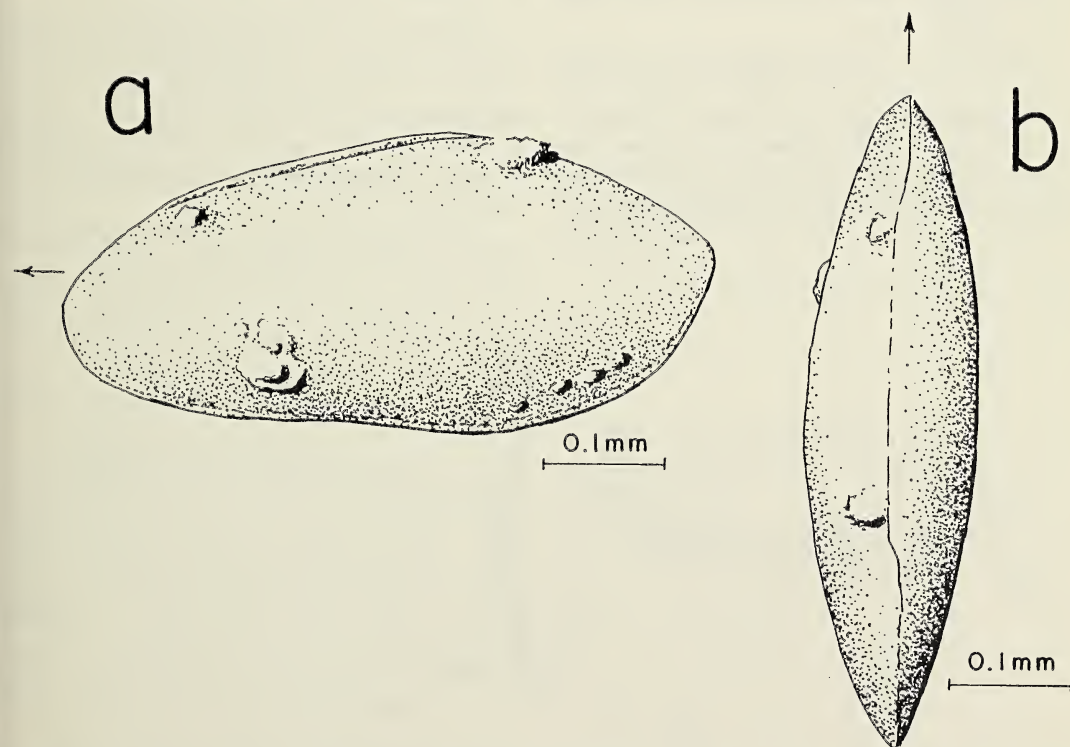
FIG. 26. *Paradoxostoma* sp. A. *a–b*, Specimen USNM 648784; *a*, left valve lateral view showing overlap of right valve; *b*, dorsal view.
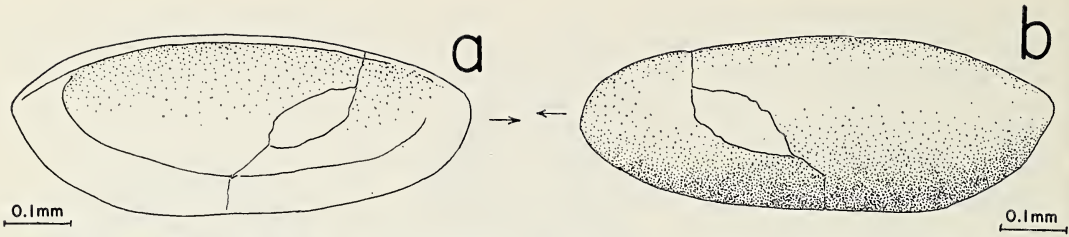
FIG. 27. *Paradoxostoma* sp. B. *a–b*, Specimen USNM 648785; *a*, internal view of broken left valve; *b*, exterior view.

Paradoxostoma cf. *P. rubrum* G. W. Müller, 1894

   Figs. 28 *a–c*

DESCRIPTION: In lateral view: carapace narrow; dorsum broadly arched; greatest height just behind midlength; venter slightly concave; anterior somewhat pointed; posterior with narrow caudal process; surface smooth; in dorsal view: posteriorly pointed, less pointed anteriorly; greatest width midlength. Duplicature wide, especially in anterior.

DIMENSIONS: Specimen USNM 648786 (broken right valve) T-4: length, 0.58; width, 0.07; height, 0.18.

DISTRIBUTION: As fossil from T-4 (1 valve). *Paradoxostoma rubrum* Müller, 1894 occurs with calcareous algae in the bay of Naples.

DISCUSSION: The extremely thin, low carapace with duplicature suggests that the species belongs in the family Paradoxostomatidae. Though placed in the genus *Paradoxostoma*,

following Müller (1894), the present specimen, together with *P. rubrum* Müller, may warrant new generic status.

   The fossil specimen from Hawaii is comparable, but not conspecific, with *Paradoxostoma rubrum* Müller, 1894 from the Gulf of Naples, Italy. These two forms are certainly closely related and differ only in details of shape.

Genus *Sclerochilus* Sars, 1866

Sclerochilus sp. A

   Figs. 29 *a–b*

DESCRIPTION: In lateral view: shell elongate, length $2\frac{1}{2}$ times the height; dorsum broadly and evenly rounded; anterior abruptly rounded, subtruncate; anteroventer concave, posteroventer slightly convex; surface completely smooth. Internal features not preserved; hinge apparently adont.

DIMENSIONS: Specimen USNM 648787 (left
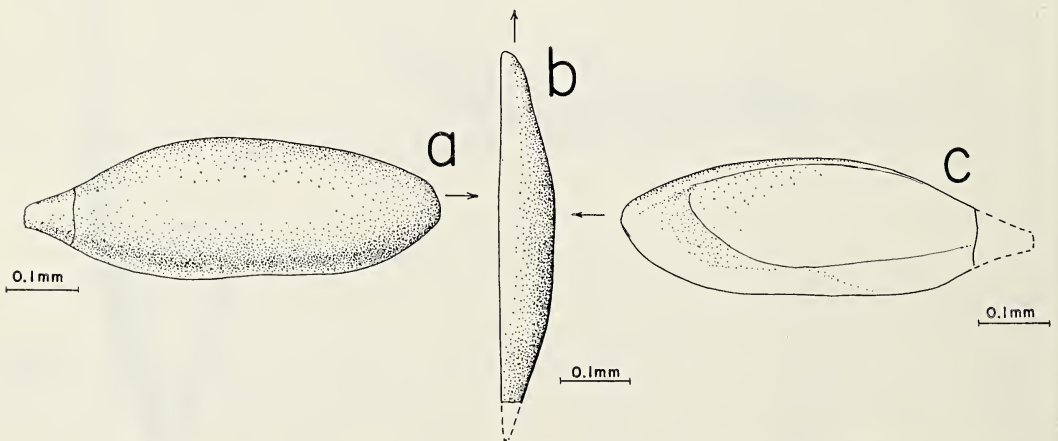
FIG. 28. *Paradoxostoma* cf. *P. rubrum* G. W. Müller, 1894. *a–c*, Specimen USNM 648786; *a*, side view of right valve; *b*, dorsal view; caudal process broken; *c*, internal view showing wide anterior duplicature.
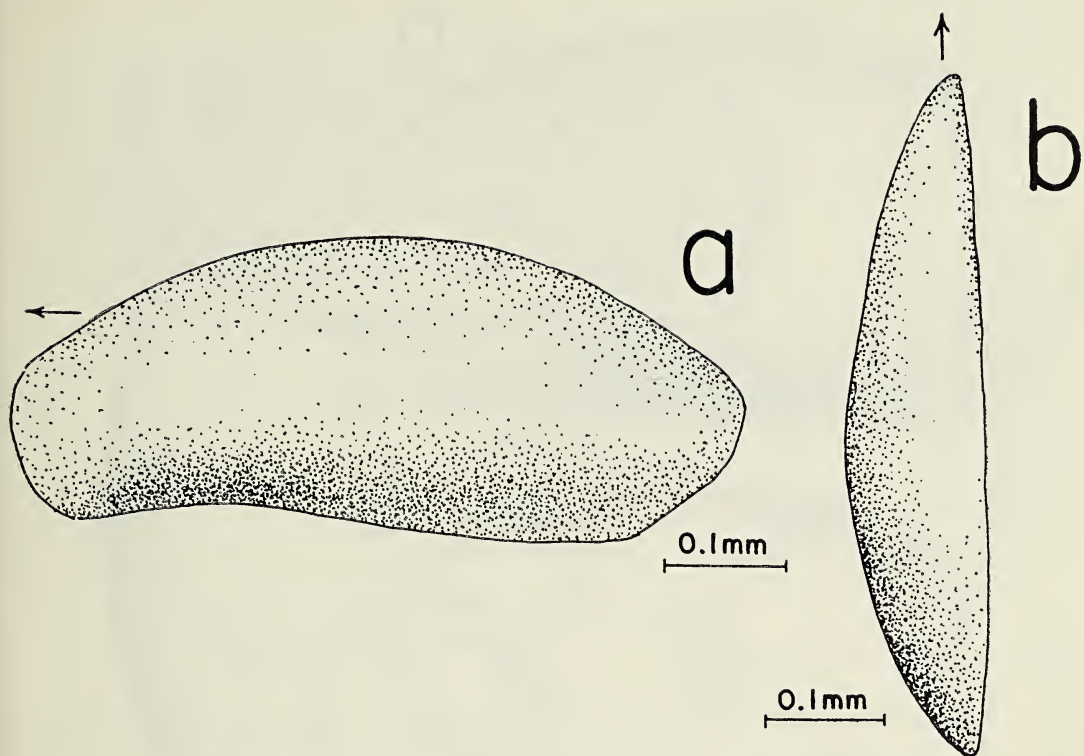
FIG. 29. *Sclerochilus* sp. A. *a–b,* Specimen USNM 648787; *a,* lateral view of left valve; *b,* dorsal view.

valve) T-12: length, 0.61: width, 0.10; height, 0.26.

DISTRIBUTION: As fossil from T-12 (1 valve).

DISCUSSION: Only one specimen of this species was collected at station T-12. The interior of the specimen is heavily encrusted, and so most certainly it belongs to the fossil suite.

Sclerochilus sp. B.
　　Figs. 30 *a–c*

DESCRIPTION: In lateral view: subovate; dorsal margin broadly rounded; anterior and posterior margins equally rounded; ventral margin gently convex in posterior half, sharply concave in anterior half; greatest valve height central; length not quite twice the height; surface smooth. In dorsal view: greatest width central; length $2\frac{1}{2}$ times the width; posterior half somewhat more inflated than anterior half.

Hinge weak: right valve apparently overlapping left valve at dorsal extremities; faint groove in right valve to receive dorsal edge of left valve. Duplicature of even width. Adductor muscle scar pattern of five elongate scars subcentrally located, all apparently divided; two oblique mandibular scars near venter above inturned area.

DIMENSIONS: Specimen USNM 648788 (right valve) T-12: length, 0.46; width, 0.10; height, 0.25.

DISTRIBUTION: As fossil from T-12 (1 valve).

DISCUSSION: The Hawaiian species bears some affinity to *Sclerochilus contortus* (Norman), 1862 of Brady, 1880 from the Recent of Kerguelen Island, southern Indian Ocean, and from Head Island, New Zealand. The two species differ only in that the former is relatively higher. Brady's forms, in turn, differ considerably from Norman's illustrations by being shorter and with more evenly rounded ends.

The single right valve dealt with here is poorly preserved. The adductor muscle scar pattern appears to be divided; however, this cannot be said with certainty.
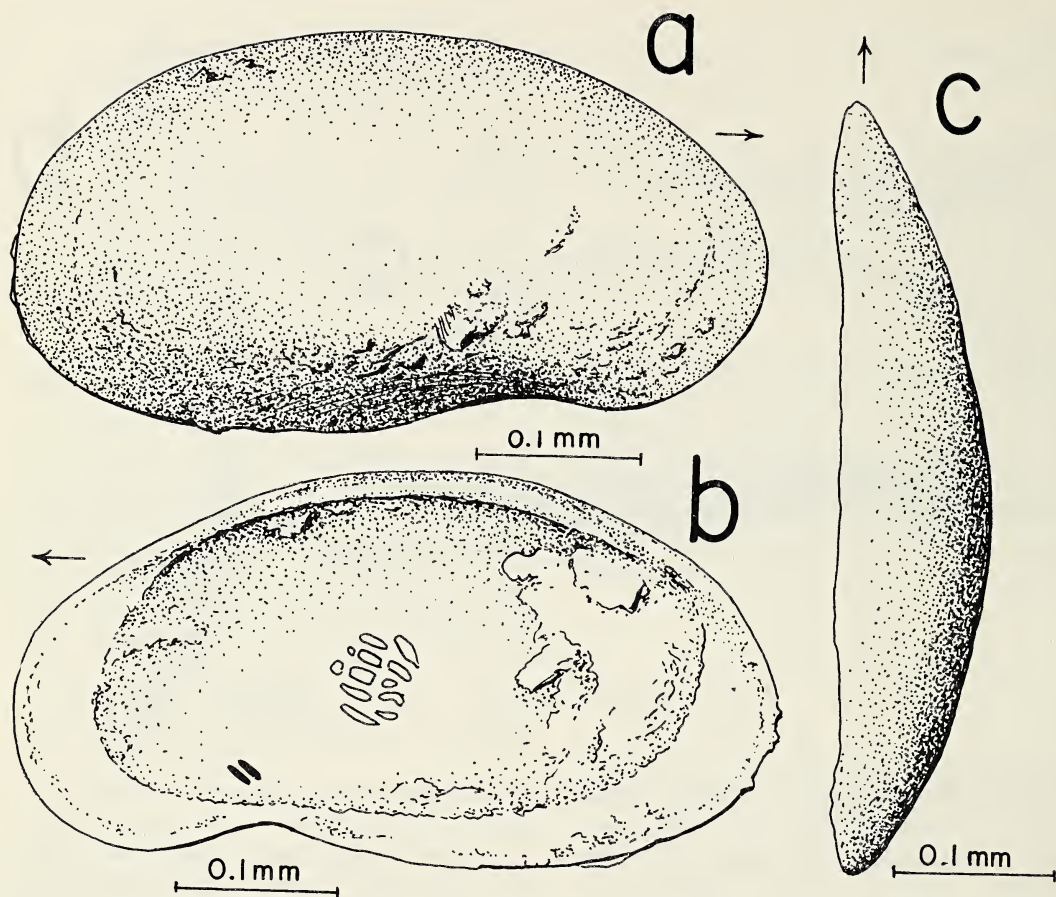
FIG. 30. *Sclerochilus* sp. B. *a–c,* Specimen USNM 648788; *a,* lateral view of right valve; *b,* internal view; muscle scar pattern poorly preserved; *c,* dorsal view.

Family TRACHYLEBERIDIDAE,
Sylvester-Bradley, 1948
Genus *Cletocythereis* Swain, 1963

Cletocythereis bradyi n. sp.
Figs. 31 *a–c*

Cythere rostromarginata Brady, 1880 [*partim*]. Rept. Voyage *Challenger,* Zool. 1, pt. 3, p. 83, pl. 16, figs. 2 *a–d.*

DESCRIPTION: In lateral view: carapace subrectangular; anterior margin bluntly, evenly rounded, denticulate; dorsal and ventral margins fairly straight, parallel; posterior margin concave in upper part, convex in lower part, forming point at midheight; five massive contorted spines in posteroventer; sexual dimorphism conspicuous, with longer males; small subdued subcentral tubercle and low conspicuous eye tubercles present; surface with large deep cloverleaf-shaped, flat-bottomed reticulations, widening inwardly, bounded by flat-topped ridges; anterior rim lined with closely packed, small, elongate, deep reticulations; lateral surface flat. In dorsal view: carapace arrow-shaped due to winglike extensions of ventral ridges.

Hinge holamphidont: right valve with heavy projecting anterior tooth, posteroadjacent entire socket, very finely crenulate groove (not illustrated in Fig. 31*b*) and entire faintly trilobed posterior tooth. Duplicature moderately wide; vestibules not present; continuous selvage from anterior tooth of right valve around venter to pointed posterior; muscle scars not observed.
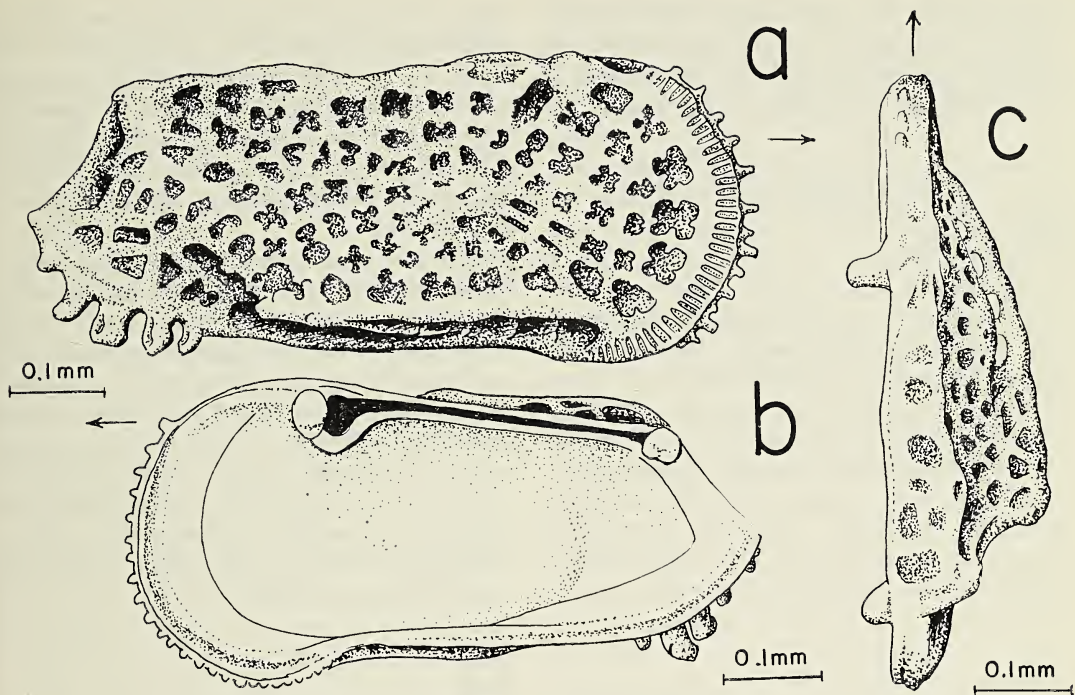
FIG. 31. *Cletocythereis bradyi* n. sp. *a,* Holotype USNM 648789; side view of male right valve. *b–c,* Paratype SDNH 1060; *b,* internal view of female right valve; *c,* dorsal view.

DIMENSIONS:

SPECIMEN	LENGTH	WIDTH	HEIGHT
Holotype USNM 648789			
(right valve ♂) T-12	0.80	0.20	0.36
Paratype SDNH 1060			
(right valve ♀) T-12	0.70	0.18	0.35
Paratype USNM 648790			
(entire ♂) T-12	0.76	0.35	0.36
Paratype USNM 648791			
(entire ♀) T-12	0.69	0.36	0.35
Paratype SDNH 1061			
(young right valve)			
T-12	0.63	0.19	0.30

DISTRIBUTION: As fossils from T-12 (13 valves; 4 entire) and Easter Island at EA-2 (4 valves; 9 entire). Reported by Brady, *partim* "females" (1880:83) at 39° 32′ S, 171° 48′ E (station 167).

DISCUSSION: Swain (1963) designated *Cythere rastromarginata* Brady, 1880 the type species of his new genus *Cletocythereis,* which, together with *C. noblissimus* Swain, 1963, from the Pleistocene Gubick Formation of Alaska, comprise the only known species of the genus. *C. noblissimus,* however, with its ornamenta-

tion of three lateral rows of spines and other differences, most probably belongs to another genus. *Cletocythereis,* to date, is monotypic.

The fossil specimens from the Hawaiian Islands are comparable in part with *Cythere rastromarginata* Brady, 1880. Brady has mistakenly equated an alate form with a compressed form, believing these differences to be caused by sexual dimorphism. Brady's inflated form (1880:pl. 16, fig. 2) and the fossils from the Hawaiian Islands are included together in the new species; his description of *Cythere rastromarginata* is obviously based on the nonalate form and it should retain the name. The present species is distinctly alate and exhibits typical trachyleberid dimorphism, with longer males. It may be significant that Brady's "males" are not reported from the same locality as his "females," but it is strange that the former were reported from the Hawaiian Islands and the latter from New Zealand.

Hermanites paijenborchiana Keij, 1957 from the Eocene of France appears to be closely related to *Cletocythereis bradyi,* differing only in

the possession of a dorsal ridge, slightly shorter carapace, and absence of ornamentation on the anteromarginal ridge. Both species show deep reticulations with secondary intergrowths.

Genus *Hermanites* Puri, 1955

Hermanites sp.
   Figs. 32 *a–c*

DESCRIPTION: In lateral view: carapace almost quadrate; dorsal margin straight, with weakly bifurcating, crooked marginal ridge; anterior margin heavily rimmed, obliquely rounded, ventrally extended; ventral straight, subparallel with dorsal margin; posteroventer with short spines; ventrolateral alae straight, horizontal, projecting posteriorly about 23° from shell; ornamentation of well-developed reticulations in a pattern concentric around large smooth subcentral tubercle; eye tubercle very large. In dorsal view: anterior blunt, with inner row of small denticles extending around entire anterior margin; posterior compressed; shell strongly projecting at subcentral tubercle, posterior part of ventrolateral ridge, and posterodorsal tubercle; carapace widest at subcentral tubercle.

Adductor muscle scars on side of deep subcentral depression; top two scars divided, elongate, oblique; two lower scars almost fused; two antennal scars on anterior side of pit; four small antennal scars on bottom of pit with large anteriorly opened V-shaped scar behind. Radial pore canals abundant, about 45 in anterior, many with elongate sinuous midswellings, coinciding with marginal denticles; normal pores sparse, not necessarily coinciding with exterior reticulations; anterior duplicature moderately wide, without vestibules.
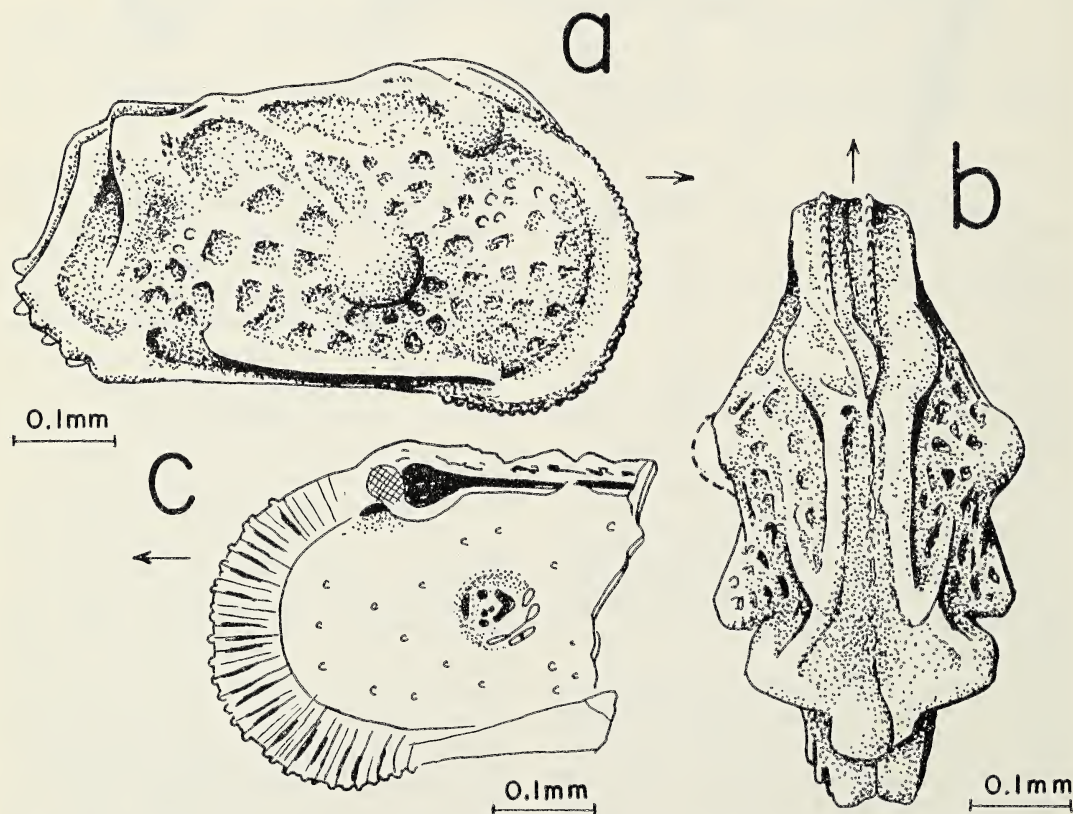
FIG. 32. *Hermanites* sp. *a–b,* Specimen USNM 648792; *a,* right valve view of entire carapace; *b,* dorsal view showing tri-tuberculate carapace. *c,* SDNH 1062; internal view of broken right valve; adductor scars in white.

DIMENSIONS:

SPECIMEN	LENGTH	WIDTH	HEIGHT
USNM 648792			
(entire) T-7	0.59	0.31	0.35
SDNH 1062			
(broken right valve) T-7	—	0.15	0.33

DISTRIBUTION: As fossils from T-7 (2 valves; 1 entire).

DISCUSSION: This species is placed in the genus *Hermanites* on the basis of morphology and ornamentation. Conversely, the internal features are unlike other species previously assigned to this genus: an excessive number of muscle scars, i.e., 6–7 antennal and 6–7 adductor scars, occurs in the present species, where typically only one antennal and four mandibular scars should be present.

Excessively divided adductor scars suggest the family Hemicytheridae; however, the radial pore canals, though abundant and with midswellings, are not as abundant as in the hemicytherids and the midswellings are irregular.

The only trachyleberid genus having excessive muscle scars is the Lower Cretaceous *Isocythereis* (Sylvester-Bradley in Moore, 1961: Q340); however, the present species does not otherwise resemble species of that genus.

Neocaudites terryi n. sp.
Figs. 33 *a–d*

DIAGNOSIS: A smooth carapace; moderate size; small knob on posterior ventrolateral surface.

DESCRIPTION: In lateral view: length about 2.1 times the height (males) to about 1.9 times the height (females); ventral margin slightly concave, curving upward at posteroventer with five or less short heavy spines; anterior margin finely denticulate, flattened in dorsal half; dorsal margin straight, sloping backward behind highest point of carapace just anterior to poorly developed eye tubercle; posterior margin truncate; left valve slightly larger and strongly overlapping right valve above eye tubercle; strong continuous marginal ridge present, angling ventrally in posterodorsal area, forming oblique lateral ridge ending at indistinct subcentral tubercle; short arcuate ridge on lateral surface just posterior to, and paralleling, anterior margin; surface smooth with faint reticulations bordering ridges and above subcentral tubercle; small pronounced knob on posterior part of ventrolateral surface. In dorsal view: carapace laterally compressed; length three times the width in both sexes; greatest inflation along
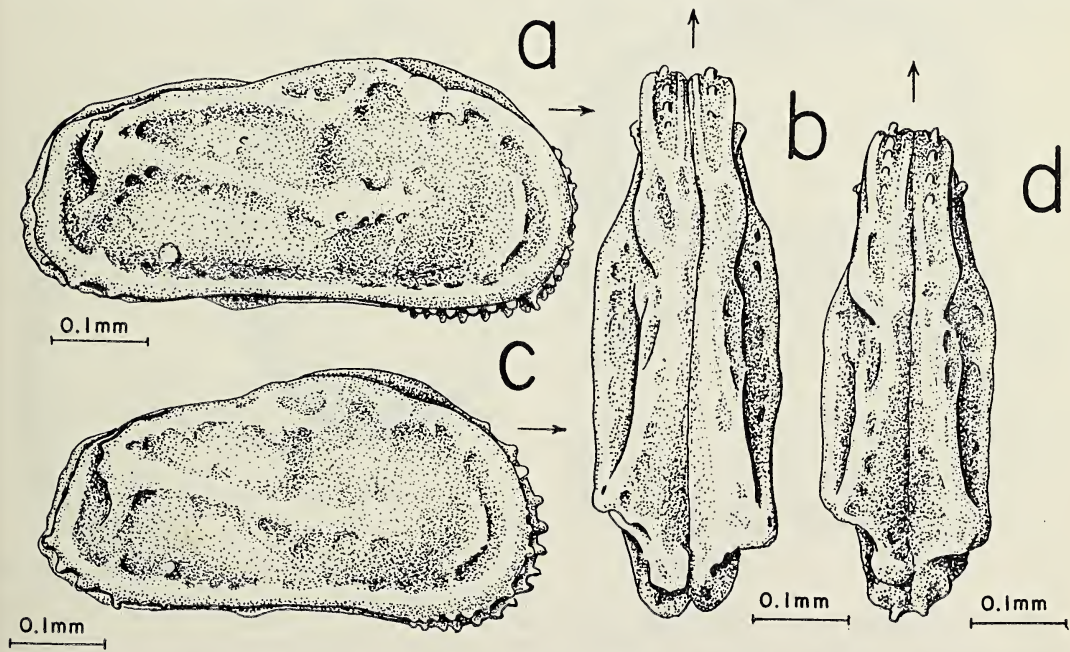
FIG. 33. *Neocaudites terryi* n. sp. *a–b*, Holotype USNM 648756; *a*, right valve side view of entire male carapace; *b*, dorsal view, Paratype SDNH 1063; *c*, right valve side view of entire female carapace; *d*, dorsal view.

median ridge; anterolateral and posterior areas compressed; valves unequal, posterodorsal rib juncture more posterior in right valve.

Hinge holamphidont: posterior tooth of right valve rounded, heavy; anterior tooth and postjacent socket large, median groove smooth. Radial pore canals abundant, muscle scars and other internal features obliterated.

DIMENSIONS:

SPECIMEN	LENGTH	WIDTH	HEIGHT
Holotype USNM 648756 (entire ♂) T-12	0.58	0.19	0.28
Paratype SDNH 1063 (entire ♀) T-12	0.53	0.17	0.28
Paratype USNM 648757 (left valve ♂) T-12	0.57	0.12	0.28

DISTRIBUTION: As fossils from T-12 (7 valves; 3 entire).

DISCUSSION: Penultimate instars of *N. terryi* are densely pitted (a finer pattern than on *N. reticulata*) and have a merodont hinge.

Named in honor of D. Terry, of North American Aviation Corporation, who collected samples T-1 through T-13.

Family XESTOLEBERIDIDAE Sars, 1928
Genus *Xestoleberis* Sars, 1866

Xestoleberis nana Brady, 1880
Figs. 34 *a–d*

Xestoleberis nana Brady, 1880. Rept. Voyage *Challenger*, Zool. 1, pt. 3, p. 126, pl. 31, figs. 3 *a–c.*

DIAGNOSIS: Greatly inflated carapace; flat venter; low, pointed anterior.

DESCRIPTION: Carapace almost oval in dorsal view: rounded posteriorly, slightly acuminate anteriorly. In lateral view: ventral margin long, straight; dorsal margin broadly rounded, sloping down anteriorly; left valve overlapping right valve around entire margin; surface smooth.

Hinge antimerodont: right valve with arcuate crenulate anterior bar, deep arcuate crenulate median furrow medially covered by thick dorsal ledge, and short, straight, heavily notched, posteriorly extending rear element.

Adductor muscle scar pattern large, of four irregular scars in vertical row; V-shaped anten-
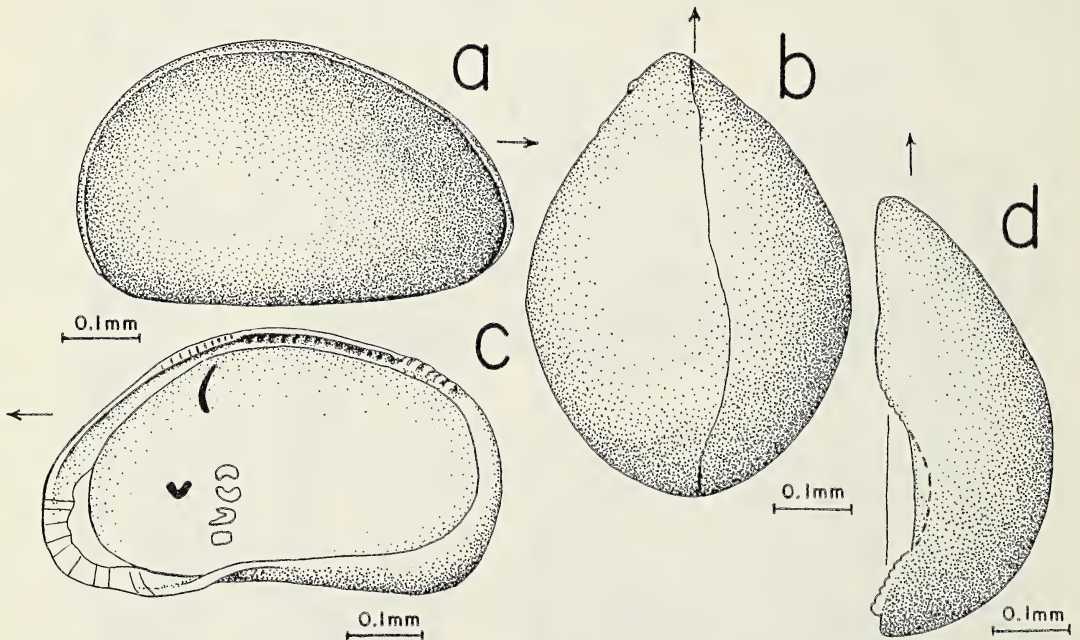
FIG. 34. *Xestoleberis nana* Brady, 1880. *a–b*, Plesiotype USNM 648767; *a*, right valve view of entire female(?) carapace showing overlap of left valve; *b*, dorsal view. *c–d*, Plesiotype SDNH 1064; *c*, internal view of female (?) right valve; *d*, dorsal view.

nal scar anterior to top two adductor scars; characteristic xestoleberid arcuate scar in antero-dorsum. Deep anterior and posterior vestibules ventrally located; radial pore canals simple, normal pores small, sparse.

DIMENSIONS:

PLESIOTYPE	LENGTH	WIDTH	HEIGHT
USNM 648767			
(entire) T-12	0.57	0.40	0.35
SDNH 1064			
(right valve) T-12	0.57	0.42	0.40
USNM 648768			
(entire) T-12	0.64	0.44	0.42
USNM 648769			
(left valve) T-12	0.62	0.27	0.39
USNM 648770			
(entire) T-12	0.57	0.38	0.35

DISTRIBUTION: As fossils from T-1 (3 valves), T-2 (4 valves), T-4 (2 valves; 1 entire), T-7 (2 valves), T-8 (3 valves), T-11 (4 valves; 3 entire), T-12 (56 valves; 3 entire), AR (2 valves; 1 entire), and S-23 (5 valves); found living from HA (1 valve) and T-13 (1 valve). Reported by Brady (1880) off Tongatabu (station 172) in the Friendly Islands.

DISCUSSION: The collection consists mostly of immature instars. Those described by Brady (1880:126) are considerably smaller (length 0.45 mm) than those dealt with here. Dr. R. H. Bate (personal communication) of the British Museum (Natural History) made comparisons of the Hawaiian specimens with Brady's types and found that *Xestoleberis nana* Brady, from the Friendly Islands, although smaller, is more similar in shape to the adult fossil specimens from the Hawaiian Islands than to their young of the same size as Brady's types.

Suborder and family uncertain
Genus *Anchistrocheles* Brady and Norman, 1889

Anchistrocheles fumata Brady, 1890
Figs. 35 *a–c*

Anchistrocheles fumata Brady, 1890. Trans. Roy. Soc. Edinburgh 35, p. 497, pl. 3, figs. 13–14.

DIAGNOSIS: Anterior margin oblique, pos-teroventrally sloping; dorsal margin nearly straight.

DESCRIPTION: Carapace smooth, laterally com-pressed, length about $3\frac{1}{2}$ times the width. In lateral view: dorsal margin gently arched, al-most straight; anterior margin subtruncate, sloping obliquely downward and backward; posterior margin broadly and evenly rounded; ventral margin concave at inturned area; left valve larger, overlapping right valve around all margins. In dorsal view: carapace lenticular; ends pointed. Moderate duplicature present; other internal features not preserved.

DIMENSIONS:

PLESIOTYPE	LENGTH	WIDTH	HEIGHT
USNM 648749			
(entire) T-12	0.61	0.11	0.30
SDNH 1065			
(left valve) T-12	0.59	0.08	0.31
USNM 648750			
(young left valve) T-12	0.45	0.10	0.27

DISTRIBUTION: As fossils from T-12 (3 valves; 1 entire). Reported by Brady (1890) as living in shore pools at Lufi-lifi, Samoa.

DISCUSSION: In every respect, the individuals from T-12 resemble those of Brady (1890: 497) from Samoa. The species was reported by Brady from only one location in the intertidal zone, but whether it is exclusively restricted to that zone is unknown.

Genus uncertain

"Cythere" caudata Brady, 1890
Figs. 36 *a–f*

Cythere caudata Brady, 1890. Trans. Roy. Soc. Edinburgh 35, p. 497.

Cythere? caudata Brady. Keij, 1954, Koninkl. Nederl. Acad. van Wetenschappen, Amster-dam, Ser. B., vol. 57, pt. 3, p. 362, pl. 3, fig. 1.

DESCRIPTION: In lateral view: carapace small (length of adult male(?) 0.41 mm), densely ornamented with oblong reticulations, whose long axes generally coincide with that of cara-pace length; dorsal margin straight; anterior margin dorsally flattened; ventral margin gently concave; posterior with a low, pointed, unor-namented, laterally compressed caudal process; broad unornamented eye spot beneath anterior
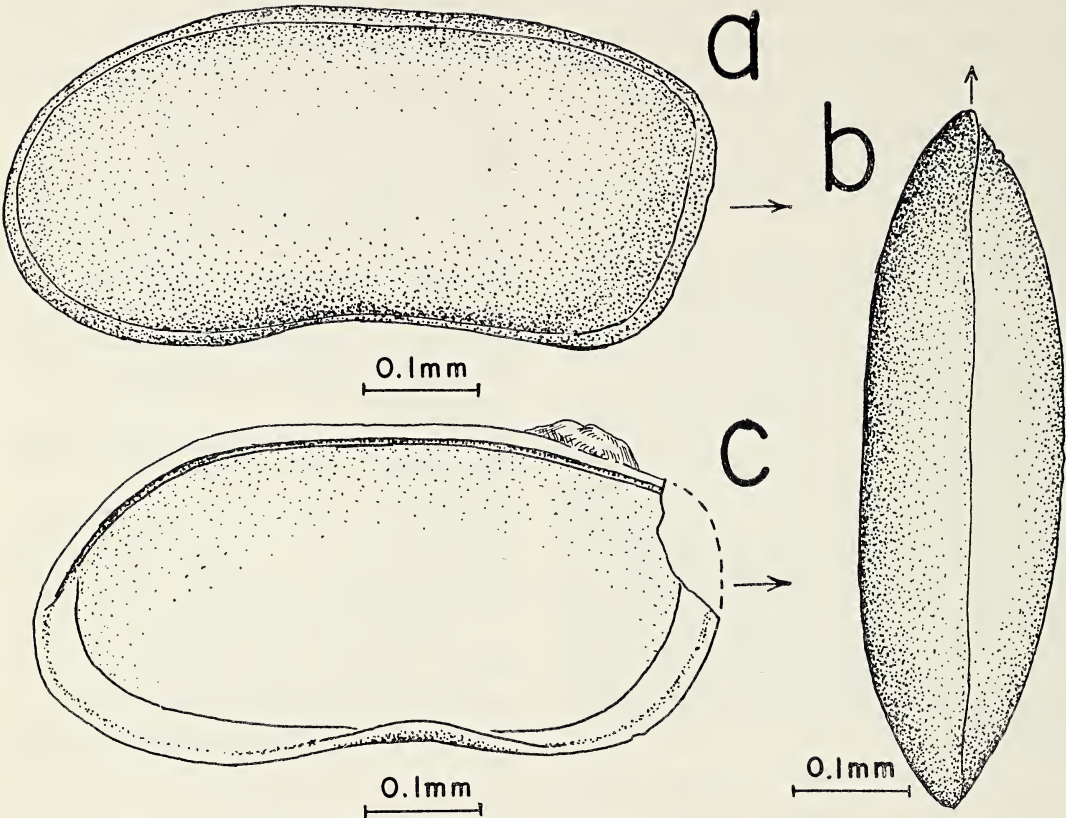
FIG. 35. *Anchistrocheles fumata* Brady, 1890. *a–b,* Plesiotype USNM 648749; *a,* right valve view of entire carapace showing overlap of left valve; *b,* dorsal view. *c,* Paratype SDNH 1065; internal view of left valve.

cardinal angle; inconspicuous curved lateral ridge roughly paralleling posterior margin. In dorsal view: carapace oblong except for compressed posterior; right valve overlapping left above hinge, overlapped by left valve above caudal process.

Hinge unique, weak: small anterior tooth of left valve faintly stepped; smooth subtle median bar; posterior element of two teeth. Anterior element of right valve a small tooth beneath socket; dorsal margin extended into faint tooth which overlaps left valve anterodorsal to socket; stepped part of anterior left valve tooth fits between two anterior teeth of right valve; posterior element single tooth posterior to, and partially above, socket.

Adductor muscle scar pattern a slightly inclined vertical row of four; single antennal scar just anterior to adductor group; single mandibular scar above adductor group. Duplicature wide; anterior vestibule deep, irregular; posterior vestibule apparently moderately deep; single and bifurcate radial pore canals extremely fine, with tendency to group; normal pores small, sparse, irregularly grouped, not coinciding exclusively with external pits.

DIMENSIONS:

PLESIOTYPE	LENGTH	WIDTH	HEIGHT
USNM 648754 (right valve) HA	0.35	0.08	0.16
USNM 648754 (left valve) HA	0.35	0.08	0.16
USNM 648755 (entire) T-1	0.41	0.15	0.17

DISTRIBUTION: As fossil from T-1 (1 entire); Recent from HA (2 valves; 1 entire). Described by Brady (1890) from Suva Suva Bay, Fiji Islands at 4 fathoms, and from Manila Bay by Keij (1954).

DISCUSSION: This species possesses features characteristic of the family Leptocytheridae; especially of the genus *Leptocythere,* with re-
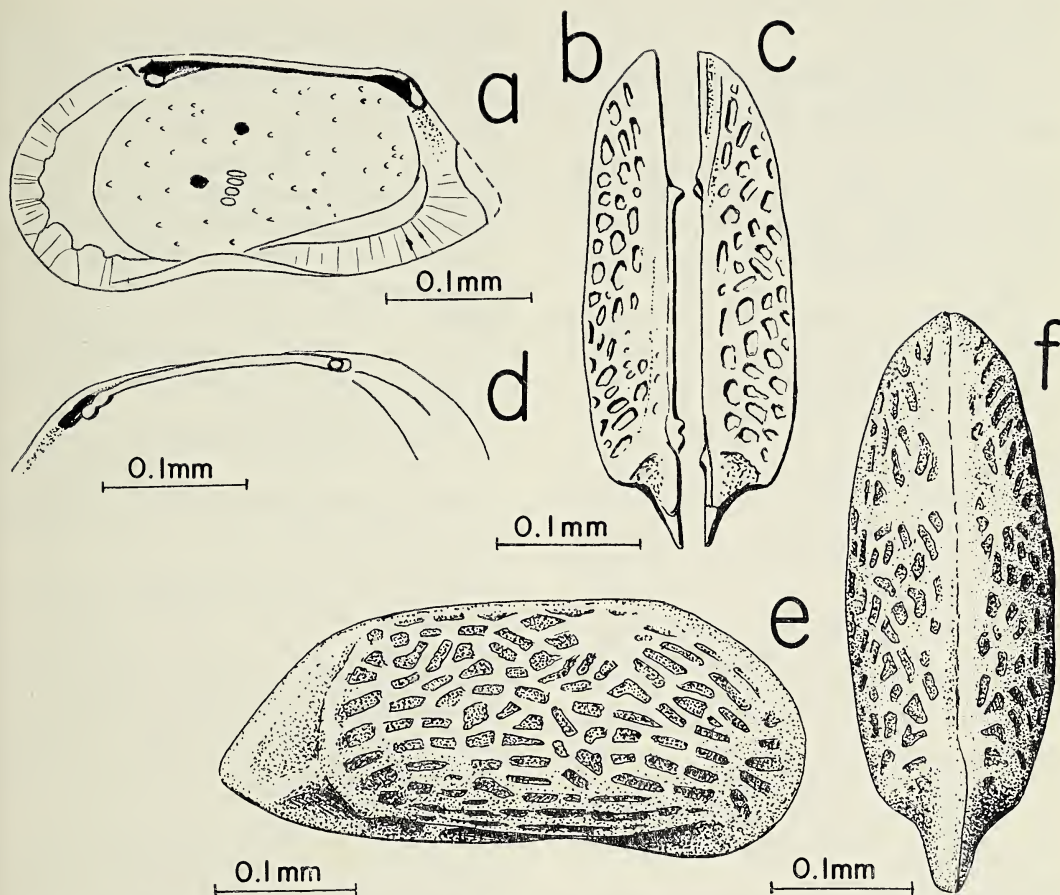
Fig. 36. "Cythere" caudata Brady, 1890. a–d, Plesiotype usnm 648754; a, internal view of broken female's(?) right valve; adductor scars in white; b, dorsal line drawing of left valve; c, dorsal line drawing of right valve; d, internal hinge view. e–f, Plesiotype usnm 648755; e, right valve view of entire male (?) carapace; f, dorsal view.

spect to its small oblong carapace and similarities in marginal areas and musculature. It lacks, however, the dentition characteristic of that family by having the median bar in the left valve instead of in the right, and by a unique tooth arrangement. Also, significant differences in the shape of the caudal process occur between "Cythere" caudata and the leptocytherids.

The fossil specimen from T-1 is longer than the living forms at HA. The long form is assumed to be the male. Hanai (1957:439) notes this type of sexual dimorphism in Leptocythere.

Slight differences occur in Brady's specimens from the Fiji Islands, but these do not appear to be important enough for specific differentiation. The greatest difference is size: Brady's

specimens are 0.46 mm in length, whereas the Hawaiian forms are much shorter. Also, the anterior margin of Brady's form is more evenly rounded; the anterior, in dorsal view, more acuminate. Keij's (1954) illustrations appear much like the Hawaiian specimens, with the exception of internal features.

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Trapezia and *Tetralia* (Decapoda, Brachyura, Xanthidae) as Obligate Ectoparasites of Pocilloporid and Acroporid Corals[1,2]

Jens W. Knudsen[3]

THE OCCURRENCE of marine invertebrates in the branches of living and dead corals has long been recognized. Two crab genera, *Trapezia* and *Tetralia,* of the family Xanthidae are determined by Garth (1964) as being obligate commensals of the coral families Pocilloporidae and Acroporidae, respectively. Crane (1947) lists species of the genus *Trapezia* as being found only in pocilloporid corals along the west coast of tropical America. Miyake (1939), in listing the Brachyura of Micronesia, records *Trapezia cymodoce* as collected from *Stylophora,* a pocilloporid coral. Garth's original collecting techniques used at Eniwetok Atoll, Marshall Islands, were refined in his later collecting in July 1959, at which time he segregated each collection of coral by species to avoid mixing coral commensals found therein.

From 10 collections of acroporid coral Garth extracted two species of *Tetralia* (*T. glaberrima,* also taken once on *Pocillopora damicornis,* and *T. heterodactyla*), but found no specimens of *Trapezia.* Conversely, from 14 collections of pocilloporid corals he obtained five species of *Trapezia* (cymodoce, f. ferruginea, digitalis, danai, rufopunctata), but obtained only one specimen of *Tetralia.* Because of this rather exclusive distribution of the species of *Trapezia* and *Tetralia,* Garth rightly concludes that these are obligate commensals of long standing. Garth states (1964:142), "In general, the larger forms were found in the more robust Pocilloporidae, the smaller forms in the more delicate Acroporidae. Thus, the *Trapezia* species occurred in the pocilloporid corals, the *Tetralia* species in the acroporid corals, although *Tetralia*

was found once in *Seriatopora,* a finely branching member of the Pocilloporidae in which the spatial relationships found in the Acroporidae obtain." Thus Garth suggests a basis of crab size and coral spatial relationships as a possible basis of this "obligatory commensalism."

The writer spent four months at the Eniwetok Marine Biological Laboratory, from February through May 1965, in order to work on crab ecology and to determine the possible basis for this seemingly ironclad crab-coral relationship. Several possible theories seemed worth investigating in order to ascertain the factors upon which this commensal-host relationship is maintained: (1) the crab-size coral-space relationship suggested by Garth; (2) that some oceanographic condition (water temperature, currents, wave action, etc.) is coincidentally required by both the crab genus and its respective host coral, therefore making the relationship one of convenience; (3) that the crab genera may prove to be filter-feeders utilizing the same food required by their host corals, thus making the relationship one of simple convenience; (4) that the host corals provide some special form of protection, in addition to simple hiding places, which exclusively attract the crab genera; (5) the possibility that more collections would reveal that both genera of crabs would be found almost equally on the Pocilloporidae and Acroporidae.

These five suppositions served to initiate field research. The first three (space-size, oceanography, food requirements) could be the key to the coral-crab relationship either with live or dead corals of the proper families, providing such corals were not overgrown with algae. However, supposition number four (special protection) could function only with live corals. Garth's term of obligate commensal was defined for our work as a situation where the crabs in question are obligated to live with their host corals in order to receive some benefit which

they could not otherwise obtain, but are not harmful to their coral hosts.

Crane (1947:83) and Garth (1964:142) note that *Trapezia* and/or *Tetralia* are limited in number to a single mated pair (with their young, Garth adds) on smaller coral heads, establishing a territory which they somehow protect (Garth). It must be noted, however, that the crabs have normal pelagic larvae, the megalops of which must seek out the proper species of host coral before settling and undergoing metamorphosis. Thus, hundreds of corals must be rejected by each megalops until the proper species is found. Gurney (1938:76–77) described the zoeal stages of *Trapezia cymodoce* and *Tetralia glaberrima* which he reared from adults in captivity, but made no note of the larvae being photonegative. Thus, one may assume that normal photopositive larvae would be attracted away from the coral host of the adult crab, to take up a normal pelagic existence. Furthermore, of the 306 clutches of eggs that we hatched out at the Eniwetok laboratory, 22 belonged to species of *Trapezia* and *Tetralia*. All of their larvae proved to be photopositive, thus indicating that they are pelagic in their larval development.

To test the supposition that size-space, oceanographic, or food relationships may serve as a key factor in commensalism, Experiment No. 1 was conducted in a deep pool on the ocean side of the north end of Eniwetok Island. Pocilloporid and acroporid corals attached to large but movable rocks were collected and·killed by air drying. Some of these corals were dried for three days while others were cleaned by rotting the tissue, washing, soaking out, and then air drying. Next, these corals were tagged, restocked with newly collected crabs (*Trapezia* on pocilloporid coral and *Tetralia* on acroporid coral, the normal hosts), and placed in the bottom of the pool. Controls consisted of tagged live corals which were stocked with newly collected crabs of the proper species.

After three days it was observed that all of the experimental crabs were missing from the dead corals (though some galatheid crabs had taken up residence). All crabs on the control corals were present (even when rechecked several weeks later). This suggested that either live coral or coral with the natural color (as opposed to the white color of dead coral) is required for protection.

To test the premise that coral color may be an important factor (Experiment No. 2), new corals were killed, cleaned, washed, dyed with vital stains of an appropriate color value so as to match the live corals, stocked with newly collected crabs of the proper genera, and placed back in the Eniwetok Island pool. Controls were used as in Experiment 1. After three days the stained acroporid heads lacked the *Tetralia* crabs and the pocilloporid heads lacked the *Trapezia* specimens, though some galatheid crabs and a few shrimps had taken up residence. All but one of the control crabs were found on their respective corals.

The results of Experiments 1 and 2 suggest that size-space relationship (which is the same in dead and live coral) is not an exclusive factor. Also, the oceanographic conditions of currents, wave action, water temperature, and dissolved oxygen were constant in the environment of the live and dead corals, and thus oceanographic factors and the availability of water-borne food were not exclusively responsible for the commensal association. Any of these, or other, factors could be critical in the distribution of these crabs, but the requisite of live coral appeared to be important.

To check this premise, selective collections of corals (Experiments 3–5) were made on the outer reef at the north end of Eniwetok Island. *Pocillopora danae* heads were obtained just inside the algal ridge where this coral abounds. Six buckets of completely dead coral heads of this species (Experiment 3, station 58) were collected from situations that were totally isolated from living corals. These corals yielded 16 species of crabs (to be described in another paper), but contained no specimens of *Trapezia* or *Tetralia*.

Next, live heads of *Pocillopora danae* which were partially dead and overgrown with algae, were processed as follows: Each head was snapped loose from the reef flat with a geologist's hammer and instantly lifted from the water and cleaved. The live portion with small areas of dead coral (Experiment 4, station 59 from which 14 species of crabs were obtained) was placed in one bucket, the totally dead portion (Experiment 5, station 60 with 18 species

of crabs) was placed in another bucket. This process was completed swiftly so as to prevent crab movement from one part of the head to another. Both the live and dead portions of coral included specimens of *Trapezia*.

Thus, Experiments 3, 4, and 5 suggest that *Trapezia* will dwell in dead Pocilloporidae only if a live portion is present, again suggesting that live corals are essential for the commensal relationship. Furthermore, totally live heads of Pocilloporidae (Experiment 6, station 63) yielded 17 species of crabs including 5 species of *Trapezia,* as would be expected from Garth's account and from the control results of Experiments 1 and 2.

Acroporid and pocilloporid coral heads are often found side by side in a given habitat, together with their commensals, *Tetralia* and *Trapezia,* respectively. The very low incidence of mismatched crabs and corals recorded at the time of our experimentation (one record of *Tetralia* on a pocilloporid coral, Garth, 1964: 142) prompted further field studies to determine if these crab genera display a true specificity for their coral families. Live acroporid and pocilloporid corals were collected (Experiment 7), their crabs were exchanged (*Tetralia* placed on Pocilloporidae and *Trapezia* on Acroporidae), and then were placed back in the deep reef pool. After 3 days the crabs were absent, suggesting that a true specificity does exist.

The feeding habits of the Trapeziinae were checked in the laboratory on captive animals used in reproductive studies. Attempts to serve as food either cut fish or algae proved unsuccessful for maintaining breeding animals. Brine shrimp (*Artemia*) nauplii were offered to the crabs with only apparent good results. Experimentally, however, crabs were starved 3 days in clean aquaria (Experiment 8) and then offered tremendous numbers of live *Artemia* nauplii for filter feeding. Half of these crabs were fed at night, the other half during the daytime. After a suitable feeding period had passed, the crabs were killed and the stomach contents examined. In no instance could *Artemia* nauplii, or their fragments, or other plankton, be recognized. On the other hand, *Artemia* eggs, which happened to be introduced with the nauplii and which sank to the bottom of the aquaria, were found in the stomachs of two

specimens of *Trapezia*. These experiments indicate that normal filtered food, meat baits, and algae are not the normal diet of the Trapeziinae.

Next (Experiment 9), crabs were collected in the field from their coral hosts, killed by cutting the carapace (to insure quick preservation), and dropped into solutions of 5% formalin or 75% alcohol. Under microscopic examination (430 diameters), without stain, no specimens of phytoplankton or zooplankton could be recognized. Instead, small round globules of some sort were present in the stomachs. This material was not identified or classified.

Concurrently, a series of laboratory experiments (Experiments 10–13) were initiated to gain better insight into the possible host-specificity exhibited by the Trapeziinae, and to determine the nature of their feeding habits.

For Experiment 10, two aquaria measuring 10 by 24 inches, by 18 inches deep, were set up and supplied with running seawater. Each tank was devoid of foreign material but was provided with one live pocilloporid head with three *Tetralia* and one live acroporid head with three *Trapezia* (these crabs were switched from their "preferred hosts"). The two coral heads in each aquarium were placed about 10 inches apart. After 24 hours the collective results from the two tanks showed that three *Tetralia* had migrated to acroporid coral, one remained on a pocilloporid coral, one was dead and the last was missing; all six of the *Trapezia* had moved to pocilloporid corals. This experiment demonstrated a distinct preference on the part of these crabs to seek out their preferred host coral. The data are not conclusive, but may suggest that this preference is slightly stronger in the *Trapezia* genus.

Experiment 11 utilized two identical running-seawater aquaria devoid of all foreign material. A small head of acroporid coral with five *Trapezia* was placed in one tank, while a pocilloporid coral with five *Tetralia* was placed in the second tank. No other corals were available to these crabs. After 24 hours five *Trapezia* remained on the acroporid coral (although one was dead) ; four *Tetralia* remained on the pocilloporid coral while a fifth crab (dead) was found a few inches away. These results tend to suggest that physical protection was sought here in the "wrong" coral since the proper

coral was not available. Since the writer can distinguish between most live acroporid and pocilloporid corals on the basis of odor alone, he assumes here that chemical "odor," or the absence of it, may cause these crabs to seek out their preferred host corals when they are present.

Experiment 12 repeated Experiment 10 but arranged the corals in a definite upstream-downstream relationship within the four running-seawater aquaria used. Each of the four aquaria had one acroporid coral with 4 *Trapezia* (a total of 16 *Trapezia*), and one pocilloporid coral with 4 *Tetralia* (a total of 16 *Tetralia*). Corals were placed about 10 inches apart (between the nearest opposing borders). In aquaria A and B the acroporid corals were placed upstream to the pocilloporid corals. The converse was true with aquaria C and D.

The results of Experiment 12 A and B, after 24 hours were as follows: 6 *Trapezia* moved upstream to their preferred pocilloporid corals, while 2 *Trapezia* remained on or under the acroporid coral; 4 *Tetralia* migrated downstream to their preferred acropid corals, while 4 were missing altogether.

The results, of experiment 12 C and D, after 24 hours were as follows: only 2 *Trapezia* migrated downstream to the pocilloporid corals, while 6 remained on or under the acroporid coral; 4 *Tetralia* migrated upstream to the preferred acroporid coral, 2 remained with the pocilloporid coral, and 2 were lost.

The combined results of experiment 12 show that, of the 16 crabs that did migrate, 10 moved upstream to their preferred host while 6 migrated downstream. Again, these results are not conclusive but suggest that chemical odors may enhance the location of the preferred coral host.

In Experiment 13, 3 *Tetralia* specimens were placed in each of four large running-seawater aquaria which also contained some nylon mesh netting soaked with mucus from live acroporid coral. Only 4 of the 12 test animals located the mucus-gauze "bait" after 24 hours. These experiments were considered incomplete, however, and will be continued in the future.

To test more fully the reactions of *Trapezia* (Experiment 14, using *T. f. ferruginea* and *T. f. areolata*) in its host coral *Pocillopora*, crab

specimens were starved for 3 days, then returned to live corals in small aquaria. When accustomed to the aquaria many crabs began what turned out to be feeding activities. The following is an account of the typical behavior displayed:

The crab climbed into the coral branches, then placed the dactyli of the walking legs (WL) 3 and 4 into polyp cups, depressing the polyps. Next, WL-1 were inserted into other polyp cups between the tentacles of the polyp, and "scratched" back and forth at a rate of about 4 strokes per second, for about 4 seconds. The tips of WL-1 were then alternately cleaned by the mouthparts of the crab. During the cleaning operation, WL-2 were used to scratch new polyps, then were cleaned by the mouthparts. Mucoid material could be seen clinging to the tips of the walking legs during this procedure.

Periodically material was transferred from WL-3 or 4 to WL-2 or 1, and then brought to the mouth. Occasionally the chelipeds were moved over the coral epidermis between the polyps. The fingers subsequently were cleaned in the mouthparts of the crab. These activities were repeated over and over again, as the crab slowly moved up through the coral branches.

Upon examining the dactyli of *Trapezia f. ferruginea,* it was noted that a special brush and comb is present on the terminal segments of each leg (referred to henceforth as the food brush and food comb). The food brushes are situated at the distal end of each dactylus (Fig. 1*E*) and consist of several short, stout, blunt-ended spines for agitating the coral polyp, and a dense tuft of bristles for collecting mucus, bacteria, and other debris. The bristle tuft is fully developed in walking leg 1 but is progressively less well represented posteriorly (Fig. 1 *A–D*). Borradaile (1903:240) figures the terminal spines of *Trapezia f. ferruginea* and suggests that "the remarkable ending of its legs is in some way connected . . . " with its life in the coral. The terminus of each dactylus protrudes ventrally, thus forming a concavity on the ventral surface of the immediate proximal part of the dactylus. The food combs, shown in the posterior view of the left dactyli (Fig. 1 *A–D*), consists of from 3 to 6 rows of
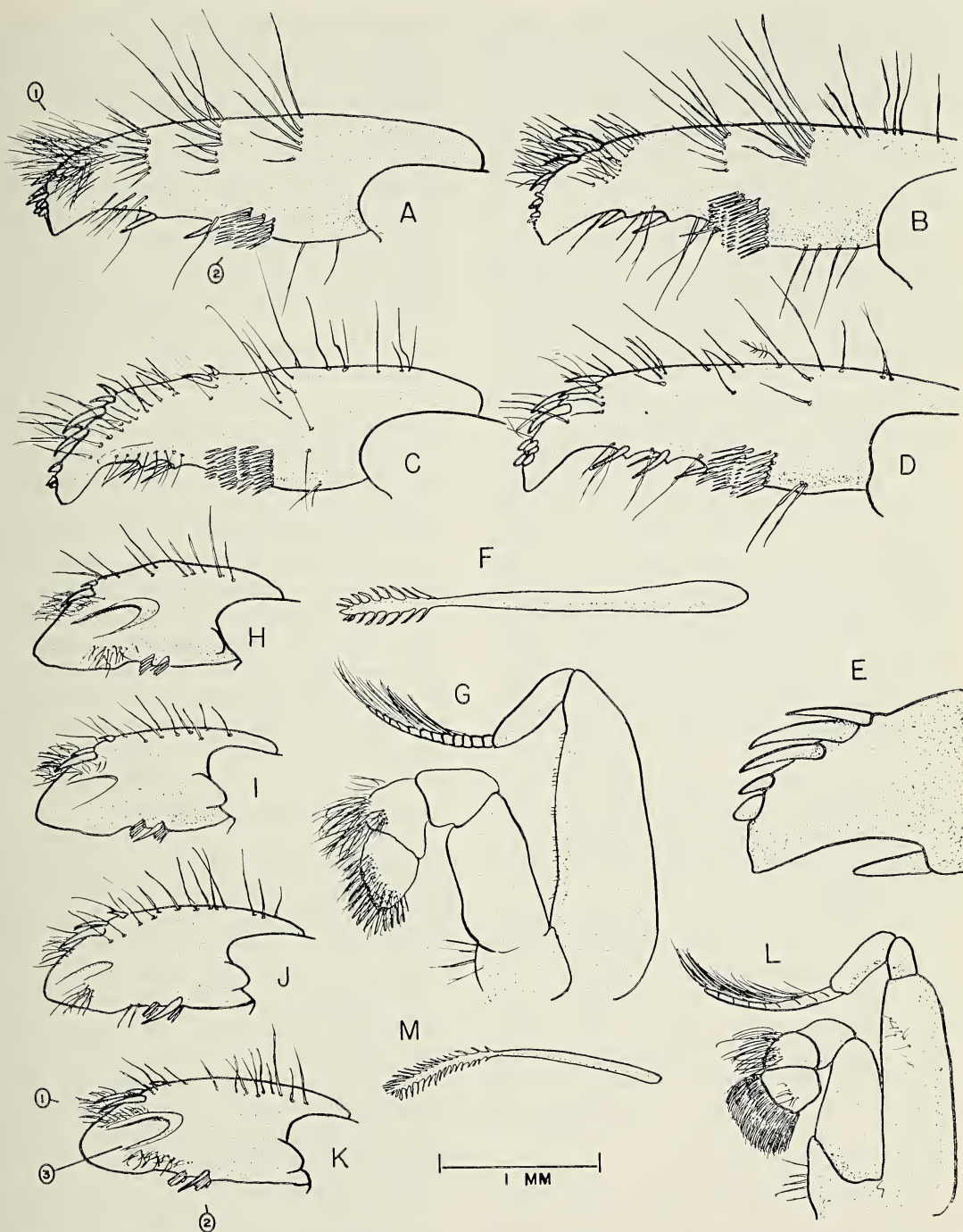
FIG. 1. *Trapezia f. ferruginea: A–D,* Dactyli 1–4; *E,* tip of dactylus 1; *F,* a bristle from food comb; *G,* 2nd maxilliped. *Tetralia heterodactyla: H–K,* Dactyli 1–4; *L,* 2nd maxilliped; *M,* a bristle from maxilliped food brush. Anatomy: *1,* food brush; *2,* food comb; *3,* groove. (All drawings to the same scale except *E.*)

feathered bristles (Fig. 1*F*) which extend under each dactylus and proceed an equal distance up the anteroventral surface of each dactylus. The combs are well developed and are presumably used in concentrating mucus from other legs, and in transferring mucus to other legs or to the mouthparts as described above. The endopodites of maxillipeds 3 are usually well bristled, and those of maxillipeds 2 have a fan of spines and dense tufts of bristles (Fig. 1 *G*) for combing food into the mouth (these are to be known as maxilliped food brushes). Furthermore, the longitudinally bifurcated basal exopodite segment of maxillipeds 1 of *Trapezia* may have a valve function to prevent the loss of food during food-transfer operations.

The dactyli of *Tetralia heterodactyla* (Fig. 1 *H–K*) have relatively small food brushes which are almost equally developed on all legs. The ventral concavity is very shallow and contains two rows of food combs consisting of flat, blunt, unfeathered bristles. These combs are almost restricted to the ventral surface of the dactylus. A conspicuous groove is also present, proximal to the end of each dactylus. These grooves are better developed on WL-1 and 4. The maxilliped food brushes of *Tetralia* are very well developed only on maxillipeds 2 (Fig. 1 *L*), and consist of dense masses of bristles which are feathered (Fig. 1 *M*) distally. The basal segment of the exopodite of maxillipeds 1 are also bifurcated as described for *Trapezia*.

Live corals, in seawater, were examined under a dissecting microscope (Experiment 15), then "scratched" as described for *Trapezia,* with a dull probe. The probe was repeatedly coated with mucus and debris from the coral animal. When examined at 430 diameters, this material proved to be identical with that material on the crabs' food brushes (Experiment 14) and with material in the stomachs of newly-killed and also field-preserved specimens.

These experiments demonstrate that *Trapezia f. ferruginea* is actually a parasite with a strong host specificity, at least on the coral family level. The presence of food brushes on other Eniwetok *Trapezia* species and on *Tetralia* species warrants recognizing them as parasites. The use of the food brushes in feeding would also explain why *Artemia* eggs were found in the stomachs of crabs offered *Artemia* nauplii for filter feeding. Presumably the eggs were transferred from the aquarium floor to the crabs' mouthparts after they had been picked up on the food brushes.

In a search of the literature for similar coral parasites, Gerlach's paper (1961:3) describes "an as yet unidentified aberrant copepod with a worm-like body which apparently lives on coral, mainly Pocilloporidae . . . . These animals could be observed as they crawled about on the surface of the coral and slashed at the tissues of the coral polyps with the sharp claws of the first pair of legs. Here the point to be considered is that this is a form which has become particularly adapted to a mode of life parasitic on coral." This behavior parallels the behavior of Trapeziinae described herein.

As to the degree of parasitism, that is, the effect of the crabs' parasitism upon pocilloporid corals, no data are available. The parasites are probably quite efficient, that is, they do not quickly kill or greatly harm their host. Otherwise, every case where numerous crabs are found occupying a coral head would result in the rapid destruction of the crabs' microhabitat. The amount of food produced for crab consumption (or the number of polyps per head) probably serves as a basis for territoriality observed by Garth (1964:142).

The coral-host preference of the two genera of crabs may well be correlated with the relative difference in size, and thus efficiency, of the food brushes and combs. This conclusion is based on the fact that when live acroporid corals are removed from seawater and placed in the shade they secrete vast quantities of mucus, while pocilloporid corals secrete little mucus under the same condition. *Tetralia,* with the smaller and less efficient brushes and combs, thus takes advantage of a coral family which presumably is capable of secreting the greatest amount of mucus. *Trapezia,* on the other hand, has larger brushes and combs but lives with a less "productive" coral family. More research is being done on this aspect.

The exact basis of the host specificity displayed by these genera of crabs may well be related to the crab-size coral-space premise suggested by Garth, or to the distinct difference in the chemical odor and probable chemical

makeup of the chief source of food, that is, the mucus secreted by the coral animals. In our collections at Eniwetok Marine Laboratory we isolated a large number of corals by species and carefully separated the parasitic and commensal crabs found therein. The identification of these animals may well reveal a more definite species-to-species relationship between crabs and corals. These data and others will be recorded in another paper, along with additional experimentation to be conducted at the Eniwetok Marine Biological Laboratory.

CONCLUSIONS

The literature, our field collections, and field experimentation confirmed that an obligate host specificity exists between the crab genus *Trapezia* and Pocilloporidae corals, and between the crab genus *Tetralia* and Acroporidae corals. Furthermore, these crabs require living corals as a source of food, in addition to protection, and should be recognized as obligate ectoparasites of their respective host corals. There may be a relationship between the food brush and comb size and the apparent ability of the two coral families to secrete mucus which governs the host preference displayed by *Trapezia* and *Tetralia*.

ACKNOWLEDGMENTS

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The Larval Development of the Sand Crab *Emerita rathbunae* Schmitt (Decapoda, Hippidae)[1]

Margaret D. Knight

Two species of the sand crab *Emerita* have been found on the western coasts of North and South America. *Emerita analoga* (Stimpson) has been recorded from Vancouver Island, British Columbia (Butler, 1959) to Magdalena Bay, Baja California, and from Salavery, Peru to Eden Harbor, Territory of Aysen, Chile (Haig, 1955). Dr. Ian Efford (personal communication of unpublished observations) has found that the northern limit of the species may be Kodiak Island, Alaska, and that the southern limit of its range in South America is the Strait of Magellan. *E. rathbunae* Schmitt has been found from La Paz, Baja California to Capon, Peru (Schmitt, 1935). Specimens of *E. rathbunae* have also been collected at San Francisquito Bay, on the east coast of Baja California above La Paz (Steinbeck and Rickets, 1941).

The larvae of *Emerita analoga* were described by Johnson and Lewis (1942). The first zoea was obtained from eggs hatched in the laboratory and one individual molted to the second stage. Later stages were described from preserved plankton samples. Larvae of the species have subsequently been cultured from egg to megalopa by Dr. Ian Efford (personal communication). During the present study, larvae of the tropical species *Emerita rathbunae* were cultured in the laboratory and compared with specimens from the plankton to provide a detailed description of the sequence of larval development and a means of differentiating the larvae from those of the amphi-tropical species *E. analoga*.

The larvae of three other species of *Emerita* have been investigated. Menon (1933) obtained five zoeal stages of *E. emerita* (L.) from the plankton, the larvae of *E. talpoida* (Say) have been described both from laboratory cul-

tures (Rees, 1959) and from the plankton (Smith, 1877), and larvae of *E. holthuisi* Sankolli have been studied in the laboratory by Sankolli (1965).

METHODS

An ovigerous female of *Emerita rathbunae* was collected from a sandy beach near La Playa, Mazatlan, Mexico, on 20 September 1963 during a cruise in the Gulf of California aboard R/V "Alexander Agassiz" of the Scripps Institution of Oceanography. The female was held aboard ship in a 3-gallon aquarium. Hatching of the eggs began 12 hours after capture. The larvae were maintained in groups of 10–25 in 4-inch glass finger bowls of 1200 cc capacity or in plastic containers of 400 cc capacity. They were transferred daily to fresh sea water and fed newly hatched nauplii of *Artemia salina* (L.). All larvae molted once during the six days' culture period aboard ship. In addition, one second zoea of the species was sorted from a plankton tow taken earlier near shore below Cape Corrientes, Mexico (19° 22′ N, 105° 03′ W), and was maintained in isolated culture aboard ship for 11 days. A surface temperature of 29.6° C and salinity of 33.9‰ were recorded for the water from which the larva was taken. The salinity of water used for cultures was 33.8–33.9‰. As the ship returned north from the collecting area, the temperature of the water held in the cultures dropped from 29° to 23° C, subjecting the larvae to considerable cooling during the early zoeal stages.

At the conclusion of the cruise, the approximately 100 larvae hatched aboard ship (then in stages II and III), and the single larva taken from the plankton were transferred to the laboratory and isolated either in compartmented plastic trays holding 50 cc per compartment, or in plastic boxes of 400 cc capacity. They were transferred daily to sea water filtered through

glass wool, and fed newly hatched *Artemia* nauplii. The laboratory cultures were maintained at room temperature which, because of seasonal cooling, decreased gradually from 22° to 19° C, with daily fluctuations of 1° C or less. The salinity range during the culture period was 33.5–33.8‰. The larvae were kept under natural illumination but away from direct sunlight.

Both aboard ship and in the laboratory, all exuviae and some specimens of each developmental stage were removed and preserved in 5% formaldehyde buffered with hexamethylene tetramine. The casts were transferred to glycerine for study. The cultures, the preserved specimens, and the exuviae were maintained in such a way that the individual history of each larva could be followed. In the course of the study, 328 exuviae and 50 specimens of reared larvae were examined and dissected.

In order to compare zoeal stages occurring naturally in the plankton with those obtained in the laboratory, 143 zooplankton samples (taken in August–September and November–December in the area between Cape San Lucas and Cape Corrientes, north into the Gulf of California to Tiburon Island, and along the west coast of Baja California north to Magdalena Bay) were examined. The majority of samples were taken with a 1-meter net towed obliquely from 140 m to the surface, filtering approximately 500 m³, during cruises 5612 (SIO Ref. 61-22, 1961), 6108 (SIO Ref. 62-16, 1962), 6208-9, Azul II and El Golfo (Snyder and Fleminger, 1965). A total of 150 specimens were obtained for comparison with cultured larvae. In addition, 70 larvae of *Emerita analoga* were sorted from zooplankton samples taken off Point Conception, on cruises 32 (SIO Ref. 52-1, 1952*a*) and 33 (SIO Ref. 52-7, 1952*b*) and off the Coronado Islands, for detailed comparison of the two species.

Larvae were dissected in glycerine. Drawings of whole specimens and appendages were prepared with the aid of a camera lucida. Young stages were stained with lignin pink to facilitate dissection and study.

RESULTS

The cultured larvae molted 7, 8, or 9 times before metamorphosis to megalopa, with the majority passing through 8 zoeal stages. The stages became progressively longer and the duration of the last stage was twice that of the preceding one (Table 1). Of the larvae cultured 42% completed zoeal development and molted successfully to megalopa. The highest mortality (20%) occurred in the terminal stage.

Within stages I, II, and III morphological development was similar for all individuals. In subsequent stages, slight variation was found among individuals that completed development in seven zoeal molts, but larvae passing through eight or nine stages showed considerable individual variation in relative growth and setation of appendages, so that the number of stages through which an individual had progressed could be positively ascertained, beyond stage IV, only by a study of its molting history. Despite this variability, the order of developmental events was similar for all larvae. The degree of growth attained with each molt beyond stage III decreased with an increase in the number of zoeal stages in the larval period, but the terminal zoeas were alike in development of appendages (addition of pleopods, growth of thoracic appendages and flagellum of second antenna, etc.) and differed mainly in details of setation and size. No larvae intermediate between the terminal zoea and megalopa were observed.

The variation among the cultured larvae in number of zoeal stages, and in morphology of individuals with similar molting histories, prompted detailed examination of specimens from preserved plankton samples. The ratios of carapace length to rostrum length (Table 2), together with study of appendages, were used for identification of planktonic specimens. The stage of development was determined by examination of the natatory setation of the first and second maxillipeds and of relative change in other appendages. The cultured larvae, hatched with four natatory setae on the exopodites of the first and second maxillipeds, added two setae with each molt through stage III. Either one or two setae were added with each successive molt. Rees (1959:368) and Sankolli (1965:39) found similar patterns of progressive increase in setation in cultured larvae of *E. talpoida* and *E. holthuisi*. Planktonic larvae of *E. rathbunae,* with rare exceptions, had only

TABLE 1

DURATION AND NUMBER OF ZOEAL STAGES FOR LARVAE COMPLETING THE MOLT TO MEGALOPA
(Means given for isolated cultures only)

NO. OF ZOEAL STAGES	NO. OF LARVAE		DAYS IN STAGE								
			I	II	III	IV	V	VI	VII	VIII	IX
Cultured larvae											
7	4	mean	–	–	–	5.3	9.3	11.5	31.8		
		range	5	5–6	4–6	5–6	8–10	10–13	22–43		
8	22	mean	–	–	5.3	6.5	9.0	8.9	12.4	30.7	
		range	5	5–6	4–6	5–8	7–11	7–12	11–16	22–43	
9	3	mean	–	–	–	7	8	9.7	9.7	13.3	29.3
		range	5	5–6	4–6	7	7–9	8–12	9–10	11–16	27–31
Planktonic larva											
8					3	3	7	8	14	?30	

Duration megalopa stage for 6 individuals: mean 12.5 days
                                                     range 10–13 days

an even number of setae on the exopodites of the maxillipeds. This setation, therefore, appeared to be a reliable indication of the number of molts through which an individual had progressed.

In samples examined, 67% of the planktonic larvae of *E. rathbunae* apparently would have molted to megalopa after six zoeal stages, 33% after seven zoeal molts. This represents, on the average, an abbreviation of the zoeal development observed in the laboratory-reared animals. Comparatively few differences were observed between individuals in comparable zoeal stages.

There were no detectable morphological differences between cultured and planktonic larvae within stages I, II, and III. In intermediate instars IV–VI, a detailed comparison of the larval cycle of seven zoeal stages, common to both cultured and planktonic forms, showed that cultured larvae were less advanced in growth and setation of some appendages than were planktonic larvae in equivalent stages. The terminal zoeas again were similar. The cultured larvae were smaller than planktonic larvae at comparable stages of development beyond stage I (Fig. A), but the distinctive proportions of the carapace and its rostral and lateral spines were consistent in both cultured and planktonic forms throughout zoeal development.

The second zoea of *E. rathbunae,* sorted from living plankton, was cultured for 7 of the 11 days aboard ship under conditions comparable with its natural environment. During this period it molted three times, following exactly the pattern of growth and setation observed in planktonic specimens preserved from the same area. The larva was transferred to the laboratory in stage V and died in stage VIII, before the molt to megalopa (indicated by segmentation of postlarval appendages visible beneath the cuticle). In stages V–VII, the rate of development of appendages was retarded in relation to the regular progressive setation (2 setae per molt) of the first and second maxillipeds. This larva developed more rapidly than did larvae hatched and cultured aboard ship which had been subjected to environmental change at an earlier age, but it was less advanced in the late instars than were larvae studied from the plankton. Although the evidence for modification of molt cycle midway in zoeal development is based on
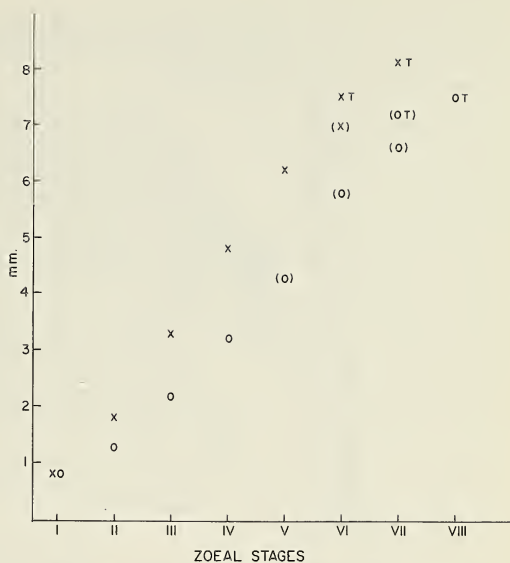
FIG. A. Average length of carapace (posterior margin to tip of rostral spine) for zoeal stages of cultured and planktonic larvae of *Emerita rathbunae*. X, Planktonic larvae; O, cultured larvae; T, terminal zoeal stage; ( ), average based on less than 10 specimens.

only a single specimen, it provides a link between the cultured and planktonic forms as well as an indication of the potential variability in the larval development of *E. rathbunae*.

Description of Larval Stages

To facilitate identification of the larvae of *E. rathbunae* in the plankton, the descriptions of intermediate stages IV and V are based upon planktonic specimens rather than upon the variable forms obtained in the laboratory. The descriptions of stages I–III and the terminal zoea are based upon both cultured and planktonic larvae for structure and development of appendages; the setation is based upon zoeal stages from the plankton. Measurements of the zoeal stages are given in Table 2. Average figures are based upon measurements of 10 or more specimens, except for zoea VI (not terminal), for which only 5 specimens were available. The length of rostrum and carapace were measured from the posterior margin of eyestalk. The length of telson excludes telson processes.

ZOEA I (Fig. 1): The zoea is colorless and translucent, the rounded carapace has a short,

TABLE 2

Measurements (in mm) of Zoeal Stages of *Emerita rathbunae*, and of Stages I–IV and the Terminal Zoea of *E. analoga* (in Italics)

STAGE	CARAPACE				ROSTRUM		LATERAL SPINES		TELSON				CARAPACE LENGTH / ROSTRUM LENGTH
	LENGTH		WIDTH		LENGTH		LENGTH		LENGTH		WIDTH		
	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE	
I	0.56	(0.54–0.60)	0.43	(0.42–0.44)	0.20	(0.18–0.20)			0.36	(0.34–0.38)	0.36	(0.34–0.38)	2.80
	0.68	*(0.66–0.68)*	*0.54*	*(0.52–0.56)*	*0.20*				*0.43*	*(0.40–0.48)*	*0.45*	*(0.42–0.48)*	*3.40*
II	0.67	(0.62–0.72)	0.62	(0.58–0.68)	1.10	(1.00–1.20)	0.56	(0.48–0.62)	0.50	(0.48–0.54)	0.49	(0.46–0.52)	0.61
	0.83	*(0.80–0.84)*	*0.77*	*(0.74–0.78)*	*1.21*	*(1.16–1.28)*	*0.65*	*(0.60–0.68)*	*0.64*	*(0.62–0.66)*	*0.64*	*(0.62–0.68)*	*0.68*
III	0.97	(0.90–1.10)	0.84	(0.78–0.94)	2.28	(2.04–2.64)	1.46	(0.90–1.70)	0.69	(0.64–0.74)	0.67	(0.62–0.72)	0.43
	1.27	*(1.20–1.32)*	*1.15*	*(1.12–1.16)*	*2.13*	*(2.04–2.20)*	*1.23*	*(1.16–1.24)*	*0.92*	*(0.86–0.96)*	*0.88*	*(0.82–0.92)*	*0.60*
IV	1.33	(1.28–1.44)	1.10	(1.04–1.20)	3.45	(3.16–3.84)	2.32	(2.12–2.72)	0.98	(0.96–1.02)	0.89	(0.86–0.92)	0.39
	1.64	*(1.52–1.80)*	*1.40*	*(1.32–1.48)*	*3.08*	*(2.84–3.40)*	*1.86*	*(1.72–2.08)*	*1.31*	*(1.20–1.36)*	*1.15*	*(1.08–1.20)*	*0.53*
V	1.75	(1.60–2.04)	1.43	(1.32–1.60)	4.41	(4.04–4.80)	3.03	(2.60–3.28)	1.34	(1.18–1.50)	1.17	(1.10–1.30)	0.39
VI	2.07	(1.96–2.16)	1.71	(1.52–1.76)	4.90	(4.80–5.06)	3.14	(3.00–3.24)	1.60	(1.52–1.66)	1.38	(1.30–1.44)	0.42
VI TERMINAL ZOEA	2.21	(1.92–2.68)	1.77	(1.52–2.16)	5.27	(4.40–5.64)	3.39	(3.00–3.88)	1.78	(1.48–2.04)	1.45	(1.24–1.66)	0.42
VII TERMINAL ZOEA	2.48	(2.24–2.64)	2.02	(1.76–2.20)	5.64	(5.40–5.89)	3.53	(3.28–3.80)	2.09	(2.06–2.14)	1.69	(1.66–1.70)	0.44
? TERMINAL ZOEA	3.45	(3.20–3.80)	2.54	(2.36–2.80)	4.88	(4.68–5.39)	2.16	(1.96–2.88)	2.81	(2.64–3.00)	2.04	(1.96–2.24)	0.71

0.5 mm
1-2

0.5 mm
3-5

Figs. 1–5. *Emerita rathbunae.* Zoea I–V.

broad rostral spine; the lateral spines characteristic of later stages are absent. The large eyes are stalked.

The first antenna (antennule) (Fig. 11) is conical and unsegmented, tapering distally to a blunt tip which bears 3 aesthetes and 2 hairlike setae.

The protopodite of the second antenna (Fig. 17) is produced into a strong lateral spine and bears a slender inner spine of approximately the same length. A small spine is situated ventrally at the base of the medial spine.

The mandibles (Fig. 23) are armed with strong ventral teeth, short triangular teeth, and slender spines. The ventral tooth of the left mandible is split shallowly at the tip. There is little change except growth during zoeal development.

The coxal endite of the first maxilla (maxillule) (Fig. 24) bears 3 terminal setae with 1 small seta subterminally on the inner margin. The basal endite bears 2 strong curved spines armed with tiny spines, the small unsegmented endopodite bears a single long seta.

The protopodite of the second maxilla (Fig. 26) is triangular, bearing 3 setae on the blunt anterior margin, 1 set slightly apart toward the scaphognathite, and 1 small seta subterminally on the inner margin. In later stages, the anterior tip becomes more pointed and the 3 setae more evenly spaced (Fig. 27). The scaphognathite bears 7–8 plumose setae on the anterior-outer margin; one-third of the specimens dissected, from both hatching and plankton, had 7 setae.

The short coxopodite of the first maxilliped (Fig. 29) is unarmed. The basipodite bears 7 setae along the medial margin in groups of 1–1–2–3 progressing distally. The endopodite is 4-segmented; the first three segments are armed along the inner margin as follows: first segment with a group of 3 setae, one conspicuously stronger than others and armed with tiny spines; second segment with 2 setae, again one being stout and armed with spinules; third segment with 2 setae spaced around the distal margin of the segment. The fourth segment bears 4 terminal setae; the outer 2 setae are quite long and armed with spinules on the inner margin. There is also a short hairlike seta placed subterminally on the outer margin which frequently curves in between the terminal setae

and is difficult to see without high magnification. The exopodite consists of 2 segments; the very short, often weakly delineated, terminal segment bears 4 long plumose natatory setae.

The coxopodite of the second maxilliped (Fig. 28) is unarmed, the basipodite bears 3 setae on the inner margin in groups of 1–2 progressing distally. The endopodite consists of 4 segments. Along the medial margin, the first segment bears 3 setae distally, the second segment bears 1 seta, and the third segment has 2 setae around the distal margin of the segment. The fourth segment bears 4 terminal setae and 1 small subterminal seta on the outer margin as described for the first maxilliped. The exopodite is 2-segmented, the small terminal segment bears 4 plumose natatory setae.

The abdomen consists of 5 segments. The first is very weakly differentiated. The sixth segment is consolidated with the telson, as shown by the position of the uropods in subsequent stages.

The telson (Fig. 34) is rounded, slightly concave, and usually about as wide as long, occasionally slightly longer than wide. There are 2 prominent posterior-lateral spines notched near the tip on the outer margin. Between the lateral spines there are 25–27, usually 26, spines around the posterior margin of the telson, with a series of very small denticles between the spines. The eighth spine from either side is somewhat longer and more prominent than the remaining spines; all are armed near the base with small spinules. There is little change throughout zoeal development except for an increase in number of denticles between the terminal spines.

In the following stages, unless noted, there is no change in setation and form of appendages described and figured for zoea I.

ZOEA II (Fig. 2): There is now a pair of short lateral spines on the carapace.

The first antenna (Fig. 12) terminates with 1 large aesthete and approximately 3 small hairlike setae.

The second antenna (Fig. 18) bears a small subterminal spine on the medial margin of the lateral spine.

The basal endite of the first maxilla (Fig. 25), with the addition of 1 spine, now bears 3 strong curved spines armed with spinules;
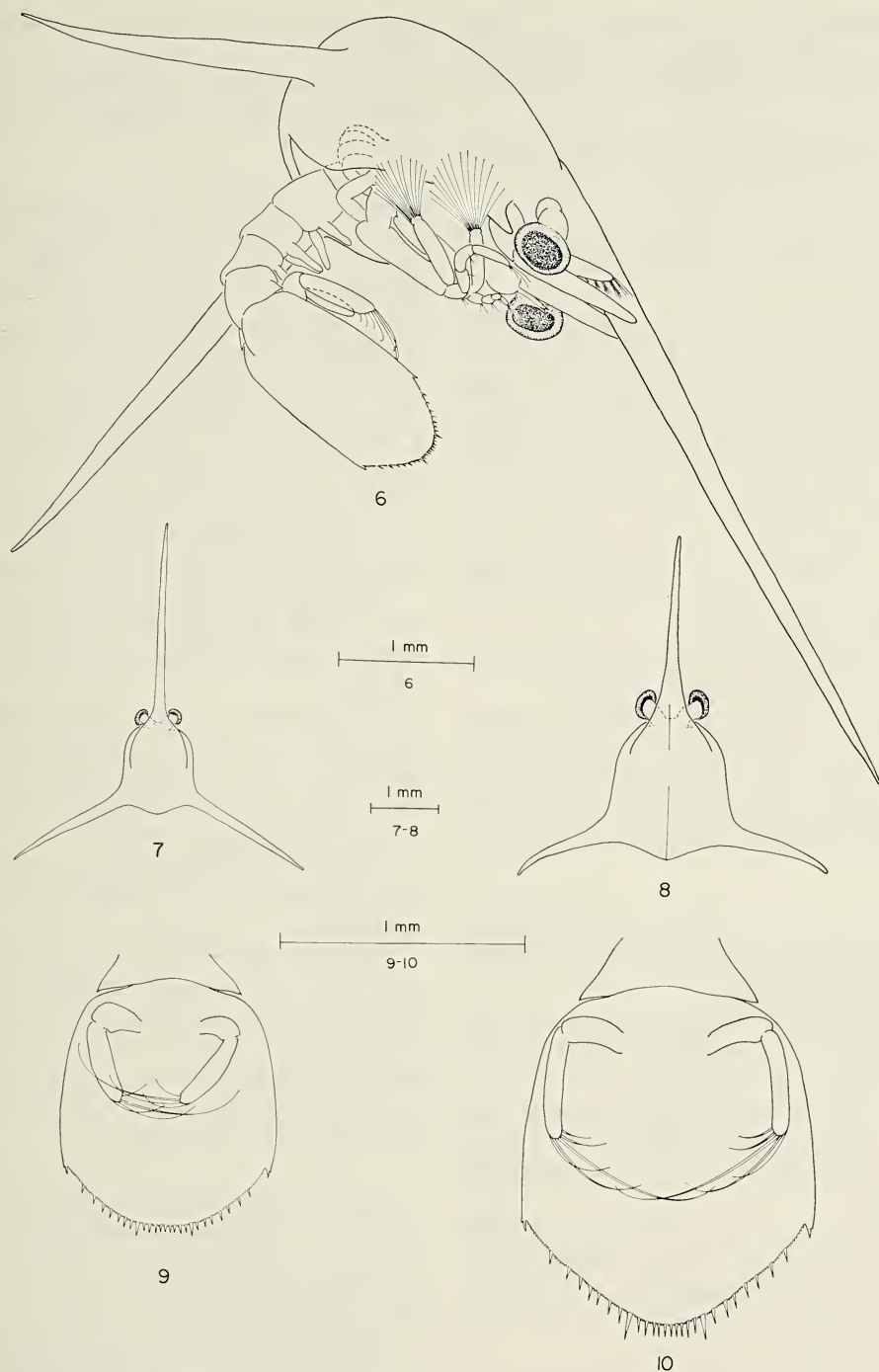
FIGS. 6–10. *Emerita rathbunae*. 6, Zoea VI; 7, zoea IV, dorsal; 9, zoea IV, telson. *Emerita analoga*. 8, Zoea IV, dorsal; 10, zoea IV, telson.

the inner two spines are articulated at the base. There is no other change and the first maxilla maintains this form throughout zoeal development.

The scaphognathite of the second maxilla bears usually 8, occasionally 9, plumose setae on the anterior-outer margin.

The exopodites of the first and second maxillipeds bear 6 plumose natatory setae.

ZOEA III (Fig. 3): The first antenna (Fig. 13) bears 3 aesthetes and 3 small setae on the tip. One aesthete is slightly larger and set apart from the other two in the terminal grouping found throughout further zoeal development.

Small spines have been added distally on both lateral and medial spines of the second antenna (Fig. 19).

The scaphognathite of the second maxilla may have 9 or 10, rarely 11, plumose setae on the anterior-outer margin.

The exopodites of the first and second maxillipeds bear 8 plumose natatory setae.

A pair of uniramous, 2-segmented uropods (Fig. 31) are now present on the anterior-ventral portion of the telson. Each of the distal segments bears 2 slender curving terminal setae armed with tiny spines distally; the inner seta is longest.

ZOEA IV (Figs. 4, 7): The first antenna (Fig. 14) now bears a subterminal tier of 2 aesthetes on the medial margin.

The flagellum of the second antenna (Fig. 20) appears in this stage as a slight rounded prominence to a small bud.

The number of plumose setae along the outer margin of the scaphognathite of the second maxilla ranged from 15 to 21; most specimens had 17–20.

The exopodites of the first and second maxillipeds bear 10 natatory setae, and the basipodite of the first maxilliped may have 8 setae along the inner margin in groups of 1–2–2–3 progressing distally.

Small buds of the third maxilliped and thoracic appendages are present beneath the carapace, posterior to the second maxilliped.

The exopodites of the uropods (Fig. 32) now bear 4 terminal setae of varying lengths; the third seta is the longest. The endopodite

may appear in this stage as a rudiment or a small bud.

The telson (Fig. 9) has become somewhat longer than wide and remains so in subsequent zoeal stages.

ZOEA V (Fig. 5): The first antenna (Fig. 15) bears usually 2, occasionally 3, subterminal groups of aesthetes along the medial margin; only one-fourth of the specimens dissected had 3 tiers of aesthetes. The majority of larvae had 4 subterminal aesthetes in groups of 2–2; rarely an additional aesthete was added to form groups of 2–3 progressing distally. Those larvae with 3 subterminal tiers of aesthetes added them in groups of 2–2–3, rarely 1–2–3.

The flagellum of the second antenna (Fig. 21) is now slightly shorter than to slightly longer than the 2 spines of the protopodite.

The scaphognathite of the second maxilla bears 24–39 plumose setae along the outer margin; most individuals had between 30 and 34 setae.

The exopodites of the first and second maxillipeds bear 12, rarely 11, natatory setae. The basipodite of the first maxilliped now bears 8 setae along the medial margin in groups of 1–2–2–3 progressing distally.

The third maxilliped and thoracic appendages have increased in size, curving under toward the thorax.

The exopodites of the uropods (Fig. 33) now bear 5 or 6 setae of unequal length; the third seta is very long. More larvae had 5 than 6 setae, a few had 5 on one side and 6 on the other. The endopodite now varies in size from a small to prominent bud approximately 1/3 the length of the exopodite.

ZOEA VI (Fig. 6): Now the first antenna (Fig. 16) usually has 4 subterminal tiers of aesthetes in groups of 2–3–4–4 or 2–2–4–4 progressing distally. Of 19 specimens 5 had only 3 tiers in groups of 2–3–4 or 2–4–4.

The flagellum of the second antenna (Fig. 22) has increased greatly in length and now dwarfs the spines on the protopodite. In specimens close to molting to megalopa, the segmentation of postlarval peduncle and flagellum can be seen beneath the cuticle.

The scaphognathite of the second maxilla
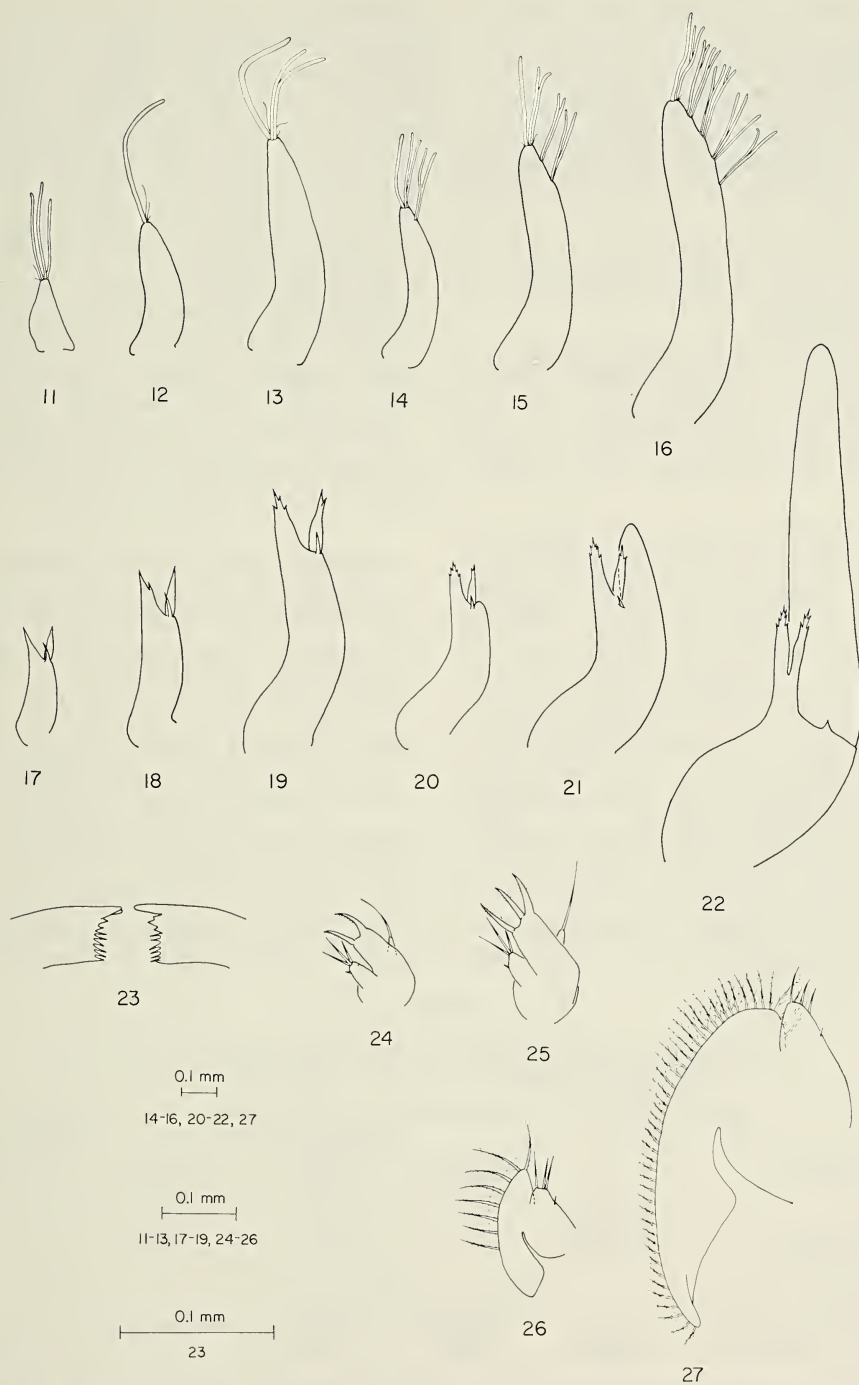
FIGS. 11–27. *Emerita rathbunae*. *11–16,* First antenna, zoea I–VI; *17–22,* second antenna, zoea I–VI; *23,* mandible, zoea I; *24–25,* first maxilla, zoea I and II; *26–27,* second maxilla, zoea I and VI.

(Fig. 27) has 43–55 plumose setae along the outer margin.

The exopodites of the first and second maxillipeds now bear 14 plumose natatory setae.

The third maxilliped and thoracic legs (Fig. 30) have increased greatly in size; the fifth leg, curved up and behind the first four, is slightly bifid at the tip.

Now each of the segments 2, 3, 4, and 5 of the abdomen bears a pair of uniramous, unsegmented pleopods.

The exopodites of the uropods (Fig. 35) bear 7 or 8 setae of varying lengths; twice as many larvae had 7 as had 8 setae; a few had both 7 and 8 setae. The endopodites are quite long, usually 3/4 the length of the exopodites.

ALTERNATE ZOEAL STAGES: Of the larvae of *Emerita rathbunae* studied from preserved samples, 49 had at least 14 setae on the exopodites of the first and second maxillipeds. While 33 of these larvae were in the described stage VI, with pleopods on abdominal somites, and were, in many cases, close to molting to megalopa, sixteen of the larvae seemed to have prolonged the larval cycle to seven zoeal stages. Five larvae with 14 natatory setae on the maxillipeds did not have pleopods on abdominal segments. They had only 6 setae on the exopodites of the uropods, 3 tiers of aesthetes on the first antenna, and in all other respects (measurements, development of appendages, etc.) were inter-

mediate between the forms described as zoea V and zoea VI. The remaining 11 larvae had 16 setae on the exopodites of the maxillipeds (one had only 15), had pleopods on abdominal somites, and were slightly larger and more advanced than the form described as zoea VI.

Two zoea IV and two zoea V were found which corresponded with the described stages in over-all proportions and in setation. They were slightly smaller, however, and some appendages were somewhat less developed (flagellum of second antenna and thoracic legs), which suggests that they might be the early stages of such an extended larval cycle.

The variation in development and setation of some appendages of cultured larvae within stage VI is summarized in Table 3.

MEGALOPA (Fig. 36): The megalopa is colorless, slightly translucid and very much like the adult in form. The most noticeable differences are presence of setose pleopods on abdominal segments and relatively large eyes. The average size of carapace in reared individuals was: length, 2.65 mm; width, 1.98 mm. No specimens from the plankton were available.

The first antenna (Fig. 37) consists of a 3-segmented peduncle and a flagellum. The second and third segments of the peduncle have small ventral processes armed with setae and that of the third segment is 2-segmented. The flagellum usually consists of 10 segments armed

TABLE 3

COMPARISON OF SOME FEATURES OF CULTURED LARVAE IN STAGE VI
FROM SERIES WITH 7, 8, AND 9 ZOEAL STAGES

FEATURE		HATCHED LARVAE			PLANKTONIC LARVA
		7 STAGES	8 STAGES	9 STAGES	8 STAGES
First antenna:	range	2	1–2	1–2	
No. of subterminal tiers of aesthetes	majority	2	2	1 and 2	3
Second antenna: Development of flagellum in relation to spines on protopodite	range	= spines	rudiment to = spines	0 to rudiment	
	majority	= spines	= ½ spines	0	= spines
First and second maxillipeds: Natatory setae	range	13–14	11–14	12–14	
	majority	14	13 and 14	12 and 13	14
Uropods: Exopod setae	range	6–7	5–7	5–7	
	majority	6	6	6	6 and 7
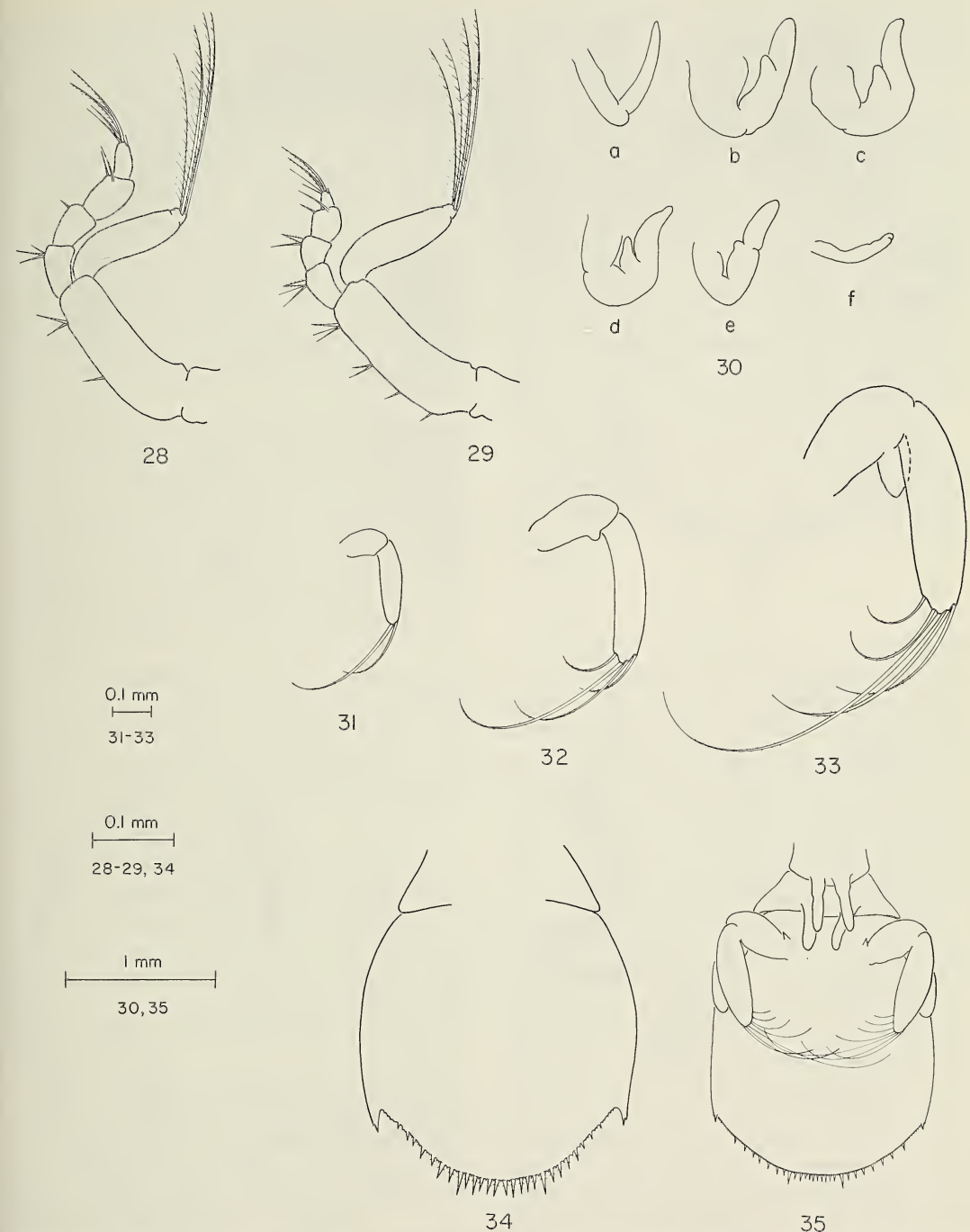
FIGS. 28–35. *Emerita rathbunae*. *28,* Second maxilliped, zoea I; *29,* first maxilliped, zoea I; *30a,* third maxilliped, *b–f,* thoracic legs 1–5, zoea VI; *31–33,* uropod, zoea III–V; *34–35,* telson, zoea I and VI.
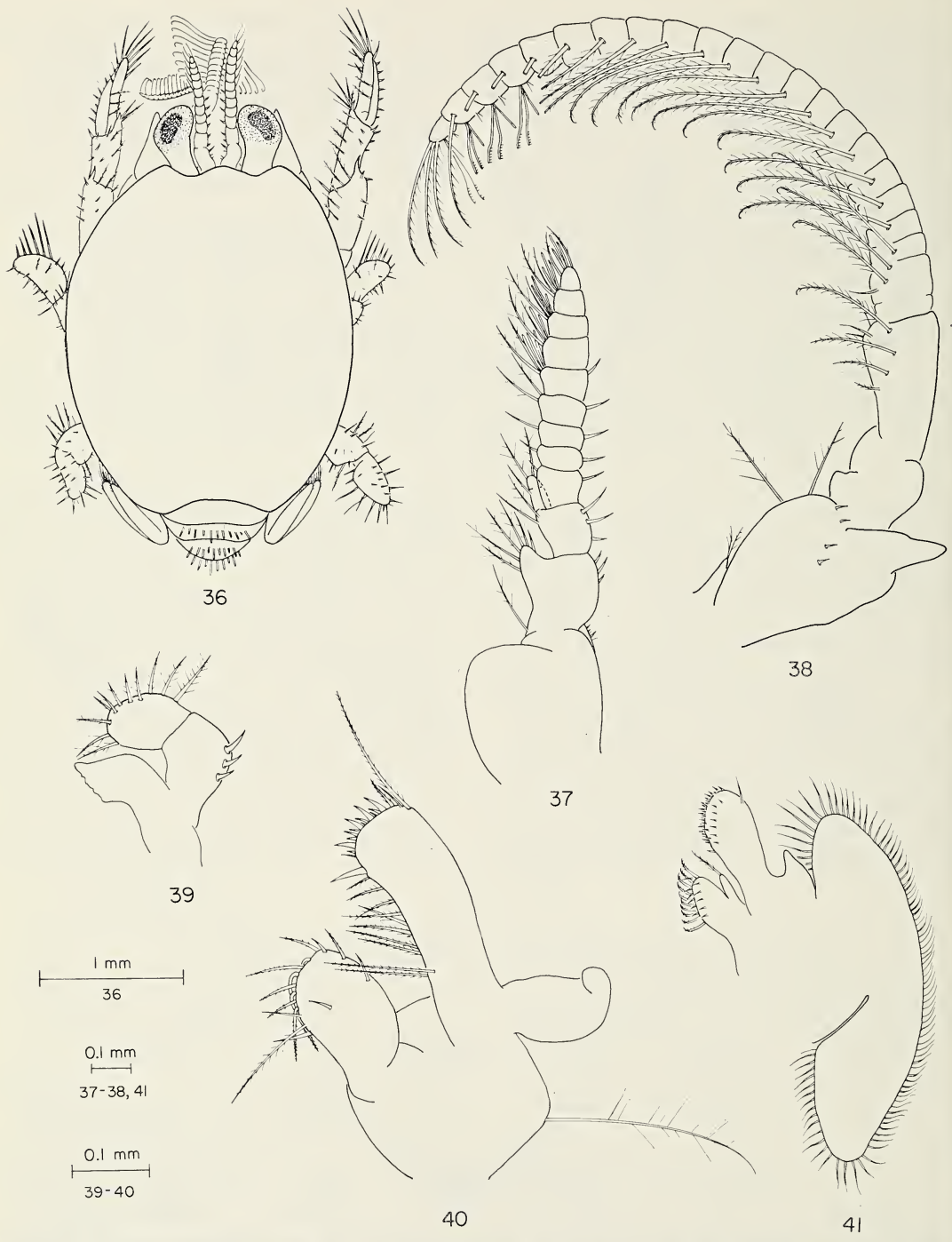
FIGS. 36–41. *Emerita rathbunae*. Megalopa. *36*, Dorsal; *37*, first antenna; *38*, second antenna; *39*, mandible; *40*, first maxilla; *41*, second maxilla.

laterally and ventrally with strong setae. The distal 5 segments bear aesthetes between the ventral setae.

The basal segments of the second antenna (Fig. 38) are similar to those of the adult. The flagellum consists of 23–25 segments each bearing 7 processes: 2 long plumose filtering setae, 2 strong setae armed with comblike spines, and 3 shorter unarmed setae.

The mandible (Fig. 39) consists of a light gnathal lobe and a palp of 2 segments. The first segment of the palp has 3, rarely 2, stout setae on the lateral margin, and the terminal segment bears setae along the medial and anterior margins.

The basal endite of the first maxilla (Fig. 40) is armed with short, stout teeth and numerous setae; 1 long plumose seta is conspicuous on the anterior-outer corner. On the coxal endite, a series of long setae curve sharply down toward the mouth region. The endopod is unsegmented and saclike. There is 1 long seta on the lateral angle of the protopodite below the endopodite.

The scaphognathite of the second maxilla (Fig. 41) has a dense fringe of approximately 95 setae along the outer margin. The coxal endite is now bilobed; the small distal lobe bears 1 long seta. The proximal lobe and the basal endite bear many setae. The small triangular endoped is unarmed.

The anterior portion of the protopodite of the first maxilliped (Fig. 42) is produced into a flat blade armed with rows of small setae and a series of long plumose setae on the basal portion. The exopodite consists of 2 segments; the bladelike terminal segment is fringed with plumose setae. The rudimentary endopod is unarmed.

The exopodite of the second maxilliped (Fig. 43) is 2-segmented; the first segment bears 3–4 strong setae on the lateral margin and the small oval terminal segment is fringed with plumose setae. The endopodite consists of 4 segments with setation as figured.

The meropodites of the third maxilliped (Fig. 44) are broad and opercular. The 3 slender terminal segments bear plumose and bristle setae; the inner surfaces are covered with dense rows of setae to form a brushlike structure.

The pereiopods are like those of the adult

in form, with the first three pairs directed forward and the fourth pair directed posteriorly. The fifth legs, slender and chelate, are curved up beneath the carapace.

The abdomen now consists of 6 segments; segments 2, 3, 4, and 5 bear biramous pleopods and segment 6 carries biramous uropods. The pleopods (Fig. 45) decrease in length posteriorly. The exopodites bear plumose setae; the first pair has 14–15 setae, the second pair bears 15–16 setae, and the third and fourth pairs have 17–18 setae. The knoblike endopodites increase in length from the first to the fourth pair and have tiny median hooks which interlock with those of the opposite pleopod to form a single swimming unit of the pair.

The oval exopodites and endopodites of the uropods (Fig. 46) are fringed with plumose and small unarmed setae. The triangular telson (Fig. 46) has plumose setae along the lateral margins.

Comparison of Species

Among larvae of *Emerita analoga* studied from preserved plankton samples, the early stages, I–IV (the "low stage IV" described by Johnson and Lewis (1942:79) with usually 10, occasionally 9 or 11, setae on the first and second maxillipeds), were found to be consistent in detail and degree of development, but later stages showed such variation in setation and development of appendages that the number of molts through which any individual had progressed could not be ascertained with confidence. The terminal zoeas, with indications of postlarval appendages beneath the cuticle, were consistent in possession of pleopods, an extremely long flagellum on the second antenna, and 5 tiers of subterminal aesthetes on the first antenna, as described by Johnson and Lewis. From 16–19 setae were found on the exopodites of the maxillipeds. Groupings of the late stage larvae by size and relative growth of appendages suggested that there were at least 7 zoeal instars in the planktonic larval life of the species.

No differences in morphological detail were detected between larvae of *Emerita rathbunae* and *E. analoga* in stages I and II. In stage III, the uropods of *E. analoga* may bear 3 setae but 7 out of 10 specimens examined had only 2
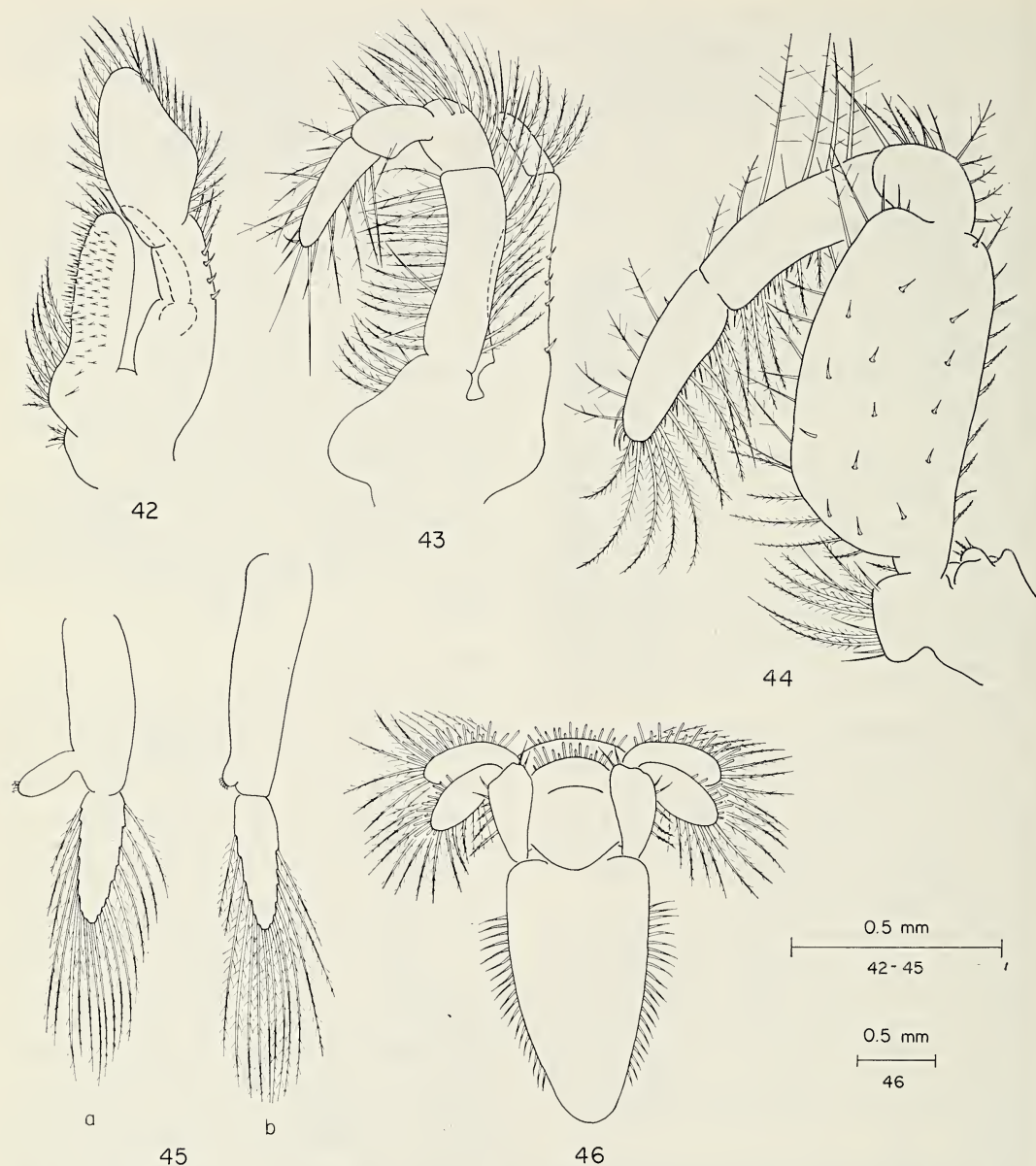
Figs. 42–46. *Emerita rathbunae*. Megalopa. *42,* First maxilliped; *43,* second maxilliped; *44,* third maxilliped; *45,* pleopods (*a,* fourth, *b,* first); *46,* uropods and telson.

setae as found in the equivalent stage of *E. rathbunae.* In stage IV, the setation of the exopodites of the uropods becomes consistent and a useful character for differentiation of the species: larvae of *E. analoga* have 5 setae and those of *E. rathbunae* have 4 setae on this appendage. In all subsequent instars, the setation of the coxal endite of the first maxilla may be used. The larvae of *E. analoga* develop a strong fifth seta subterminally on the proximal margin, while larvae of *E. rathbunae* apparently maintain 4 setae throughout zoeal development.

Differences in terms of size of carapace, ratio of length of carapace to rostral spine, and proportions of the telson increase between larvae of *E. analoga* and *E. rathbunae* as zoeal devel-

opment proceeds. The larvae of *E. anologa* become progressively larger than those of *E. rathbunae,* and the carapace spines are considerably shorter in relation to the length of the carapace. The posterior margin of the telson of *E. analoga* larvae becomes increasingly pointed and triangular between the prominent eighth marginal spines, while that of *E. rathbunae* remains smoothly rounded. Measurements of the first four stages and of the terminal stage of larvae of *E. analoga* are given in Table 2 for comparison with equivalent stages of *E. rathbunae.* The carapace and telson of both species in stage IV are shown in Figures 7–10.

The larvae of *Emerita emerita,* described by Menon (1933), and *E. talpoida,* described by Rees (1959) and Smith (1877), and those of *E. rathbunae* and *E. analoga* appear to be very similar in structure of appendages and in form of carapace and telson. The pattern of development may be common for all species through stage III, and through stage IV (with specific variation in setation) for those species described from the plankton. Larvae of *E. emerita,* and *E. talpoida* apparently pass directly from zoea IV to terminal zoea in the plankton. Those of *E. talpoida* in the laboratory and of *E. rathbunae* and *E. analoga* in both laboratory and field have a variable series of intermediate instars between stage IV and the terminal zoea in which there is progressive growth and setation without addition of appendages. The zoeal stages which appear to be common to all larvae of the genus are as follows:

1. Uropods absent

    a. Lateral spines on carapace absent, 4 natatory setae on maxillipeds . . . . Stage I
    b. Lateral spines on carapace present, 6 natatory setae on maxillipeds . . . . Stage II

2. Uropods present

    a. Pleopods absent, 8 natatory setae on maxillipeds . . . . Stage III
    b. Pleopods absent, 10 natatory setae on maxillipeds . . . . Stage IV
    c. Pleopods present, 12 or more natatory setae on maxillipeds . . . . Terminal Stage

Distribution of Larvae

The locations of zooplankton samples examined and the distribution of *Emerita* larvae are given in Figure 47. Larvae of *E. analoga* were found in samples taken near Magdalena Bay, and those of *E. rathbunae* usually in samples taken south and east of Cape San Lucas. A group of stage I larvae were found in nearshore samples from the west coast of Baja California below Magdalena Bay. From measurements, they appeared to be larvae of *E. rathbunae,* but lack of morphological features with which to differentiate stage I larvae of the two species makes identification tentative. In addition, 16 larvae of *E. rathbunae,* ranging from zoea II to terminal zoea VI, were found just south of Magdalena Bay. It seems likely, inasmuch as the range of developmental stages was found in the sample, that the larvae were hatched locally and that populations of the species might be found in the sandy beaches between Cape San Lucas and Magdalena Bay.

Twenty larvae were found in samples taken in November and December in the Gulf of California, the majority north of La Paz, which, although slightly smaller, were almost identical with those of the coastal *E. analoga* in morphological detail and proportions. Only late stages were obtained. These showed variation in setation and development of appendages similar to that found in larvae of *E. analoga.* During August to December, the movements of surface water along the western coast of Baja California are predominantly offshore and westerly (Wyrtki, 1965). It therefore seems unlikely that the larvae could have been carried into the Gulf from breeding populations near Magdalena Bay. The appearance of the *analoga*-like larvae in a series of samples suggests that either *Emerita analoga* or a closely related species may be found in the warm temperate zone of the Gulf of California, extending north from Aqua Verde Bay on the west coast and Puerto San Carlos on the east (Garth, 1955, 1960).

<center>DISCUSSION</center>

This study of planktonic and cultured larvae of *Emerita rathbunae* has shown that the number of zoeal stages in the larval period is vari-
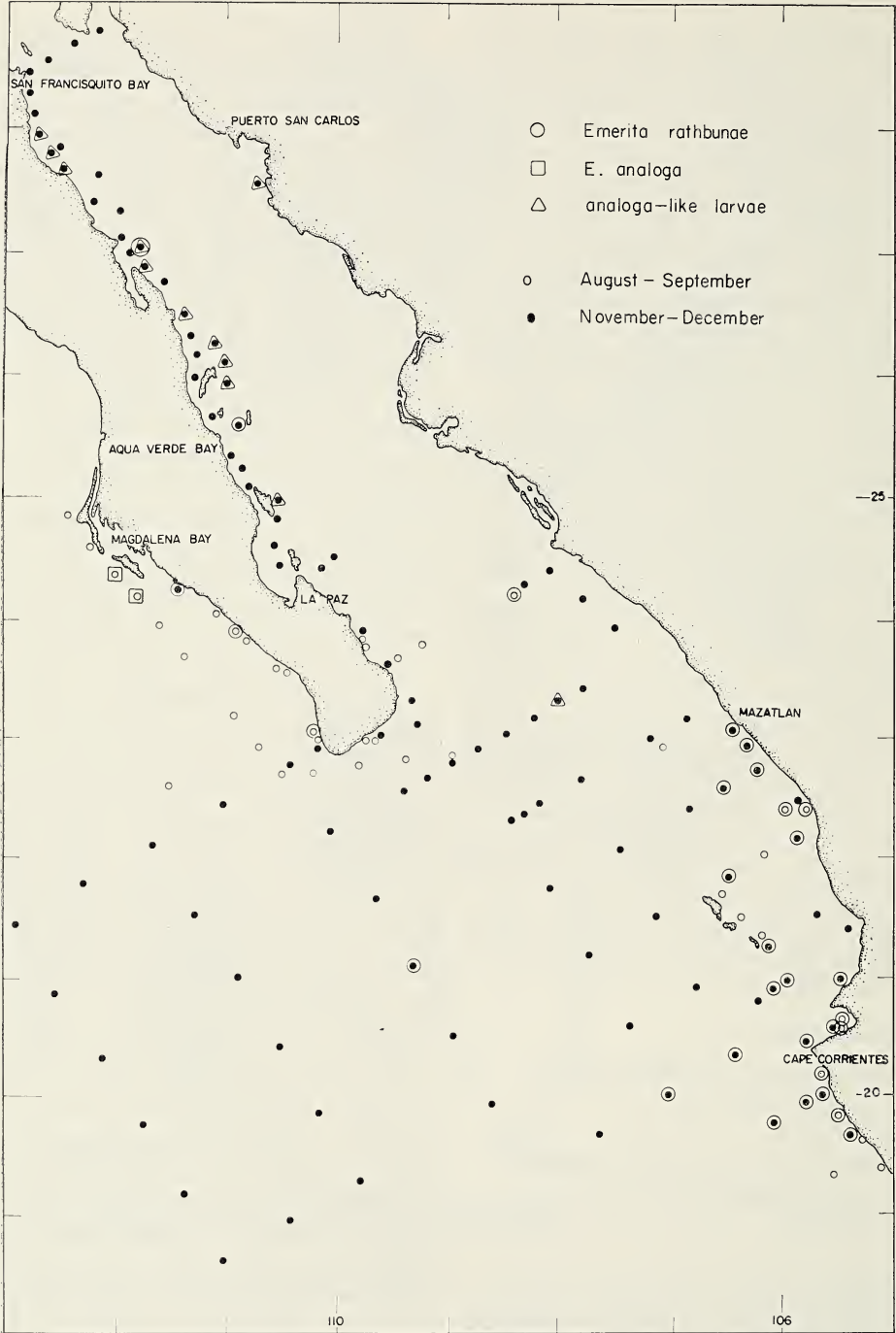
FIG. 47. Location of zooplankton samples examined and distribution of *Emerita* larvae.

able, both in nature and under conditions of laboratory culture. In the laboratory, although the larvae retained their specific proportions and pattern of development, as many as three intermediate instars could be added to the larval sequences usually observed in specimens from the plankton. Variability between individuals at comparable stages of development increased with an increase in the number of zoeal molts in the larval period.

A variable number of zoeal stages has been found in the laboratory culture of two other species of *Emerita*. Dr. Ian Efford (personal communication) has noted 9–11 zoeal molts among reared larvae of *E. analoga,* and larvae of *E. talpoida* cultured by Rees (1959) passed through 6 or 7 zoeal stages before the molt to megalopa. Rees, using setation of the maxillipeds as an indication of the stage of development, compared the zoeal stages observed in the laboratory with those described by Smith (1877) from the plankton and found that larvae from the plankton which molted to megalopa in the laboratory were apparently only in stage V. Rees noted as well that "zoea from nature possess features (appearance of thoracic limb buds, pleopods, etc.) which show them to be farther advanced in development than the corresponding laboratory stages." This relation between cultured and "natural" larvae was also observed in the present study.

Some indication of seasonal variation in number of zoeal stages was found in specimens of *E. rathbunae* examined from the plankton. Most (94%) of the late-stage larvae taken in August and September appeared ready to molt to megalopa after six zoeal stages; in the December samples only 32% would metamorphose after six stages and 68% after seven stages.

Differences in setation and development of appendages between individuals in comparable intermediate stages were not noted by Rees in cultured larvae of *E. talpoida* and were rare in larvae of *E. rathbunae* from the plankton. Individual variation became more pronounced among reared larvae of *E. rathbunae* with an increase in the number of zoeal stages, and might be related to rate of development. Larvae of *E. rathbunae* subjected at an early age to low temperatures (and perhaps other variables) of the laboratory environment had a larval span of

81–94 days. *E. talpoida* completed zoeal development in 23–33 days at 30°C. The molting frequency of the planktonic larva of *E. rathbunae* cultured through two instars at 27°–30°C was consistent with that found by Rees for *E. talpoida,* and it appears likely that *E. rathbunae* would have a much shorter larval life at the higher temperatures in its natural environment. Perhaps culture of *Emerita* larvae over a range of controlled temperatures would show a relation between duration and number of zoeal stages and degree of individual variability. The consistent difference in size found between cultured and planktonic specimens suggests that larvae of this species are restricted in over-all size by the conditions of laboratory culture.

Costlow (1965) has reviewed accounts in the literature of variability within larvae of Crustacea and has discussed effects of environmental factors (light, diet, temperature, salinity, etc.) on frequency and variability in molting, as well as current investigations of endocrine mechanisms related to molting in larvae of brachyuran decapods. Variation in number of zoeal intermolts has been noted in the laboratory culture of several anomuran decapods by Provenzano (1962*a, b*) for two species of pagurid crabs, and by Boyd and Johnson (1963) for the galatheid, *Pleuroncodes planipes,* but apparently such variation is rare among brachyurans. Gurney (1942) suggested that artificial rearing might give misleading results, and stated that, while stages I–III in the development of larval decapods seemed to be relatively fixed, the natural course of development after that might be disturbed with addition of stages not found in nature. He noted as well that there is no certainty that all stages observed in nature are passed through by all individuals of a species. The use of only laboratory-reared material to investigate the growth patterns of a species with such capacity for variability in larval development as that shown by *E. rathbunae* would indeed have been misleading unless supplemented by a study of the larvae taken from their natural environment.

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Chromatophore Responses in Relation to the Photoperiod and Background Color in the Hawaiian Ghost Crab, *Ocypode ceratophthalma* (Pallas)[1]

Georgiandra Little[2]

THE FUNCTIONAL ACTIVITIES of chromatophores are classified as morphological when there is a change in the amount of pigment present over a period of time, and as physiological when there is a relatively rapid change due to changes in the degree of dispersion of the pigment. A primary chromatophore response is a response to a nonvisual stimulus, while a secondary response is a response to a visual stimulus (Fingerman, 1963:8).

The most common method of describing the degree of dispersion of the chromatophore pigments is that of Hogben and Slome (1931:12, fig. 1) using a one to five scale, where one corresponds to maximum concentration and five to maximum dispersion of the pigments, and the intermediate stages are described as two, three, and four.

The present study deals with the ability of the Hawaiian ghost crab, *Ocypode ceratophthalma* (Pallas), to maintain a rhythmic physiological chromatophore response with different periods of light and darkness and on different backgrounds.

The author wishes to thank Dr. Ernst Reese at the University of Hawaii and Dr. John D. Costlow, Jr. and Dr. Edward C. Horn at Duke University for their kind assistance and many helpful suggestions.

MATERIALS AND METHODS

Male and female ghost crabs were collected from three different areas on the island of Oahu, where the beaches are composed of very fine sand presenting a white background. Large crabs, with a carapace length of more than 22 mm, and medium crabs, with a carapace length of less than 22 mm, were collected. A length of 22 mm was chosen as the dividing point between large and medium crabs because ghost crabs begin to develop eye stiles, a characteristic of mature crabs, when they reach a carapace length of more than about 20 mm (Crane, 1941:303). Several attempts were made to use small crabs with a carapace length of less than 12 mm, but these tiny crabs almost always died within 18 hr, making any prolonged experimentation impossible. Since no apparent difference was observed in the chromatophore responses of the two crab sizes, the results have been combined.

Crabs were caught either at night or shortly after dawn by chasing them with nets or by digging them out of their burrows. They were placed immediately in individual 8 × 4 × 4 inch plywood boxes with $\frac{1}{2}$ inch mesh wire tops, filled about $\frac{3}{4}$ inch deep with sand. These crabs were returned to the laboratory within an hour after collection, and a petri dish of sea water was put in each box.

Within 8 hr after return to the laboratory the crabs were placed on one of the following regimes.

White background, normal photoperiod
White background, reversed photoperiod
White background, constant darkness
White background, constant illumination
Black background, normal photoperiod
Black background, reversed photoperiod
Black background, constant darkness
Black background, constant illumination

During an experiment the animals' black chromatophores on the proximal, anterior surface of the third walking leg were indexed, using the Hogben and Slome (1931) indexing

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scale at 6-hr intervals with the aid of a Kyowa dissecting microscope ($\times 45$) and a Spencer illuminator. The crabs were kept in their individual wooden boxes with a petri dish of sea water to which fresh sea water was added every 6 hr if needed. They were fed daily, either a small bit of raw meat or bread soaked in milk.

The normal photoperiod was daylight and nighttime with the animals kept outside the laboratory. Two indexing time patterns were used. The 0600, 1200, 1800, 2400 sequence provided three indexing periods in daylight and one in the dark. The 0500, 1100, 1700, 2300 sequence provided two daylight and two dark indexing periods. The animals in constant darkness were kept in a dark closet and were exposed to the light only for the few seconds it required to index their chromatophores every 6 hr. A 15-watt Westinghouse cool white fluorescent light in the closet was used to maintain the animals in constant illumination with the animals kept at a distance of 3.5 ft from the light source. The artificial light and the dark closet were also used to reverse the normal photoperiod by keeping the animals in the dark for 12 hr during the day and turning on the light for 12 hr at night.

White sand from Oahu's beaches provided the white background used in the experiments. Black sand from the island of Hawaii, originating from black lava, was used in the experiments where a black background was needed.

As a final experiment an attempt was made to see if the observed chromatophore responses were the result of visual stimuli. Medium crabs were collected and maintained on a white background. In half of these crabs the eyestalks were completely covered with dark red Revlon nail polish. The eyestalks of the other half of the crabs were covered with clear Revlon polish. The animals were kept outside the laboratory in the normal photoperiod and their chromatophores were indexed every 6 hr at 0600, 1200, 1800, 2400.

RESULTS

The data are presented in Figures 1–6. Time of day is given on the abscissa, and the chromatophore rating scale of Hogben and Slome (1931) is given on the ordinate. Unless otherwise indicated, 10 crabs were used for each experiment. The data have not been treated statistically.

In the normal photoperiod, using the indexing times of 0600, 1200, 1800, and 2400, 20 crabs maintained on a white background displayed a daily rhythmic chromatophore change with maximum pigment dispersion at 0600 and minimum dispersion at 2400 (Fig. 1). The 20 crabs maintained on a black background under the same light conditions displayed a daily rhythm with a peak at 1200 and a low point at 2400 (Fig. 1), though they displayed much less marked response. Crabs on a black background were generally darker at any hour.

Crabs were maintained under the same light conditions with the chromatophores indexed at 0500, 1100, 1700, and 2300 in order to have two indexing periods in the dark (2300 and 0500) and two periods in the light (1100 and 1700). Crabs on white sand maintained a rhythmic change where a peak was reached during the day and a low point at 2300, while crabs on black sand displayed a daily rhythmic change with a similar pattern of peaks and low points (Fig. 2), but with less total variation. These crabs were generally darker at all times.

As shown in Figure 3, crabs maintained in the reversed photoperiod showed a reversal of their daily rhythmic changes. The crabs were in total darkness for 12 hr, including the 1100 and 1700 indexing times, and in constant artificial light for 12 hr, including the 2300 and 0500 indexing times. On both black and white backgrounds the crabs displayed more pigment dispersion in the simulated daytime than in the artificial night. In comparing the reversed (Fig. 3) and normal (Fig. 2) photoperiods, the 0500, 1100, 1700, 2300 normal photoperiod results have been used so that both experiments have two indexing times in the light and two in the dark. Comparison of the chromatophore indices of crabs during the two photoperiods showed that the peaks of the normal photoperiod occurred simultaneously with the low points of the reversed photoperiod and vice versa, indicating that the chromatophore rhythms were reversible. Crabs maintained on white sand displayed this reversal more distinctly than crabs maintained on black sand. Crabs on a black background displayed a greater degree of pigment dispersion at all times.

FIG. 1. The average daily indices of the darkly pigmented chromatophores in *Ocypode ceratophthalma*. The crabs were maintained in the normal photoperiod for 3 days on a white or a black background. The chromatophores were indexed every 6 hr.

FIG. 2. The average daily indices of the darkly pigmented chromatophores in *Ocypode ceratophathalma*. The crabs were maintained in the normal photoperiod for 3 days on a white or a black background.

FIG. 3. The average daily indices of the darkly pigmented chromatophores of *Ocypode ceratophthalma* when the crabs were maintained in the artificially reversed photoperiod for 4 days on a black or white background.
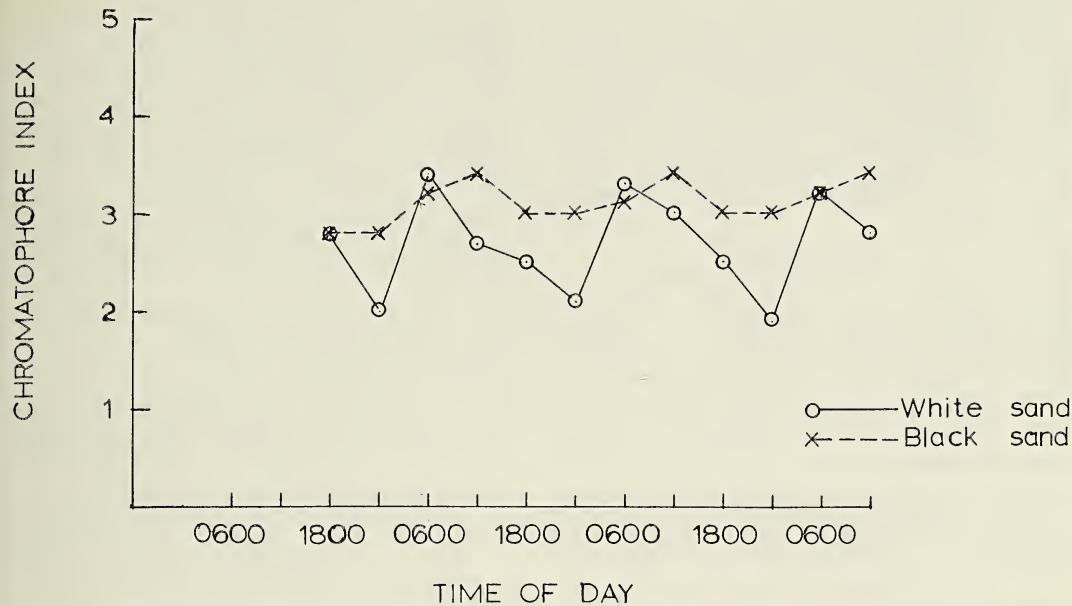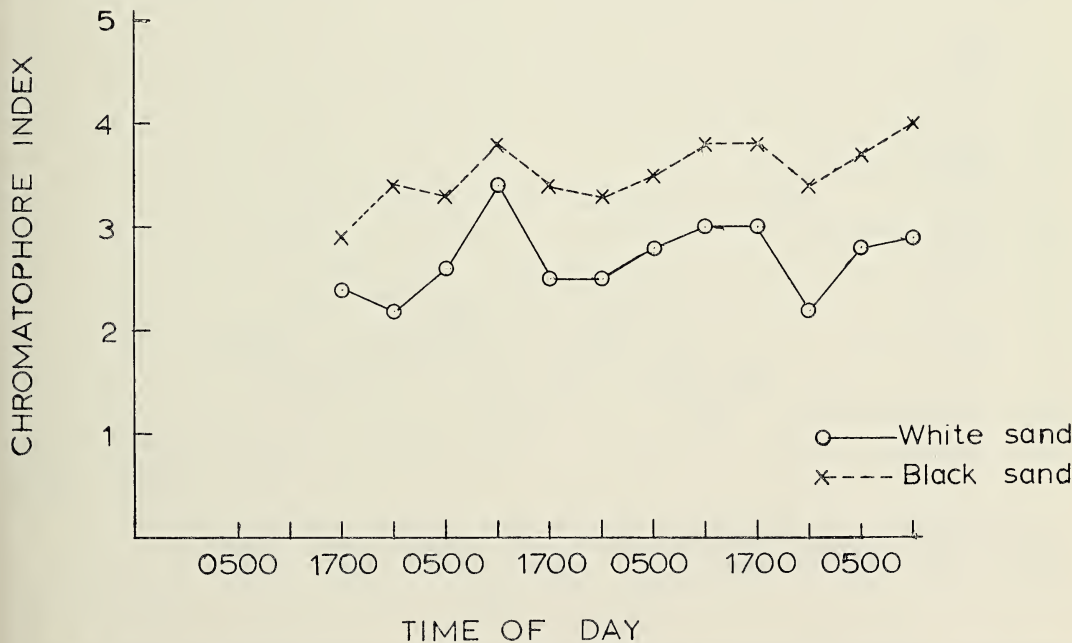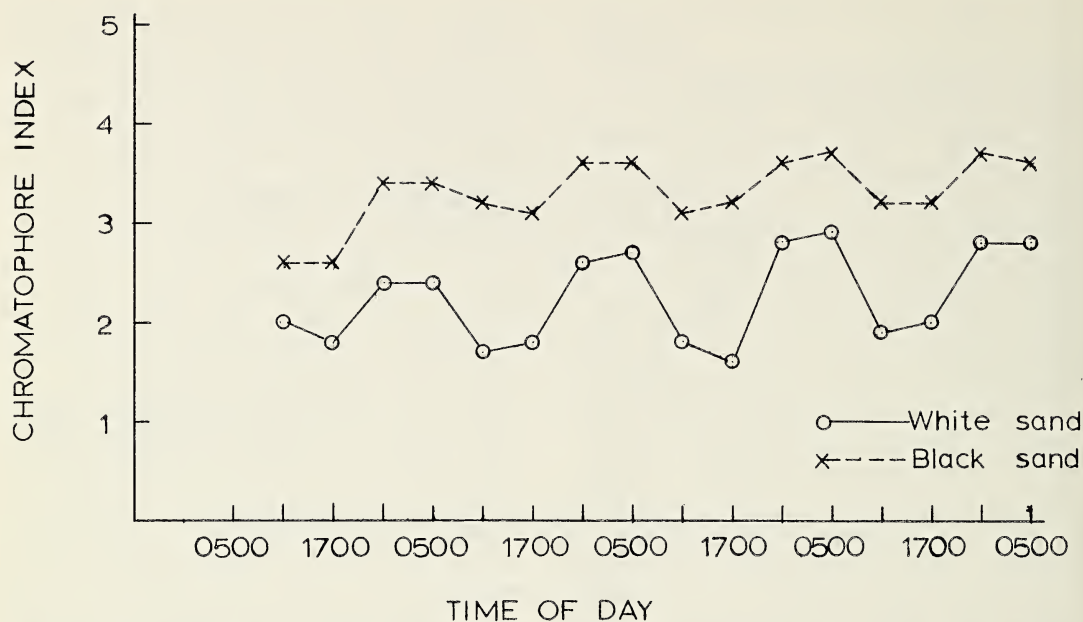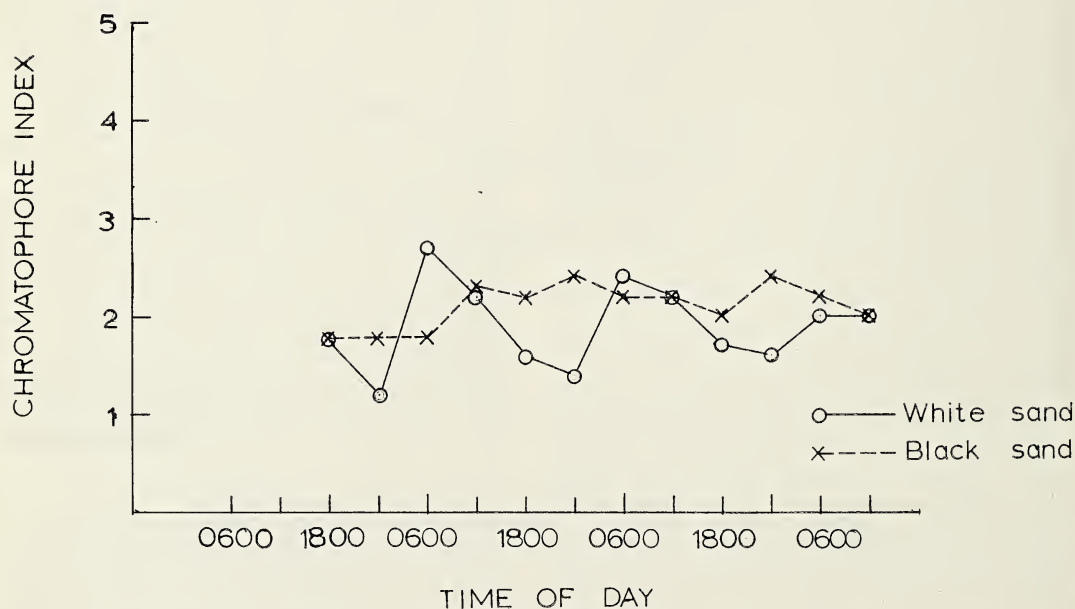

FIG. 4. The average daily indices of the darkly pigmented chromatophores in *Ocypode ceratophthalma* when the crabs were maintained in constant darkness for 3 days on a black or a white background.

Figure 4 shows the results of maintaining crabs in constant darkness. In crabs maintained on white sand a daily chromatophore change rhythm similar to the one displayed during the normal photoperiod was observed, though it was at a lower level on the Hogben and Slome (1931) scale (compare with Fig. 1). The chromatophore rhythm of crabs maintained in constant darkness on black sand became irregular (Fig. 4).

When crabs were maintained on a white background under constant illumination, a small rhythmic chromatophore change was observed the first day, but then it began to decay. In crabs maintained under similar light conditions on a black background the rhythm died out (Fig. 5). As in preceding experiments, crabs on the dark background displayed a consistently greater degree of pigment dispersion.

Figure 6 shows the results of covering the eyestalks of medium-sized crabs with either dark red nail polish or clear nail polish and maintaining them on a white background in the normal photoperiod. When the chromatophores were indexed at night, the two observed indices were very close, but when the chromatophores were indexed in the light, the crabs with the clear nail polish on their eyestalks showed a greater degree of pigment dispersion (Fig. 6), at least during the first two days. Toward the end of the experiment the difference in response between the two experimental groups diminished appreciably. This phenomenon was attributed to chipping of the red nail polish.

DISCUSSION

Other studies have been conducted on the existence of persistent rhythmic physiological chromatophore changes. An endogenous rhythm in the fiddler crab *Uca* has been reported by Brown and Sandeen (1948:370). The persistence of this rhythm in total darkness has been tested (Brown, Fingerman, Sandeen, and Webb, 1953:36), and Webb (1950:336) found that the rhythm could be altered by artificially changing the normal time of night and day.

The results obtained in these experiments suggest that the Hawaiian ghost crab exhibits a daily rhythm of chromatophore changes under normal conditions, with maximum concentration of the dark pigment at night and maximum dispersion of this pigment during the day. In most chromatic decapods the dark pigment in
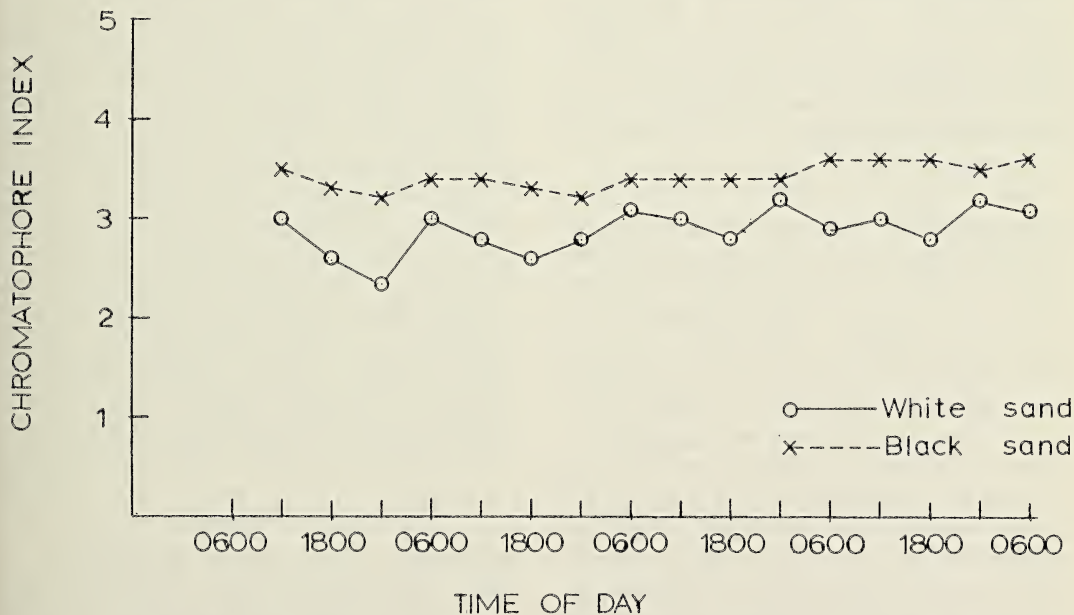

FIG. 5. The average daily indices of the darkly pigmented chromatophores in *Ocypode ceratophthalma* when the crabs were maintained in constant fluorescent illumination for 4 days on a black or a white background.
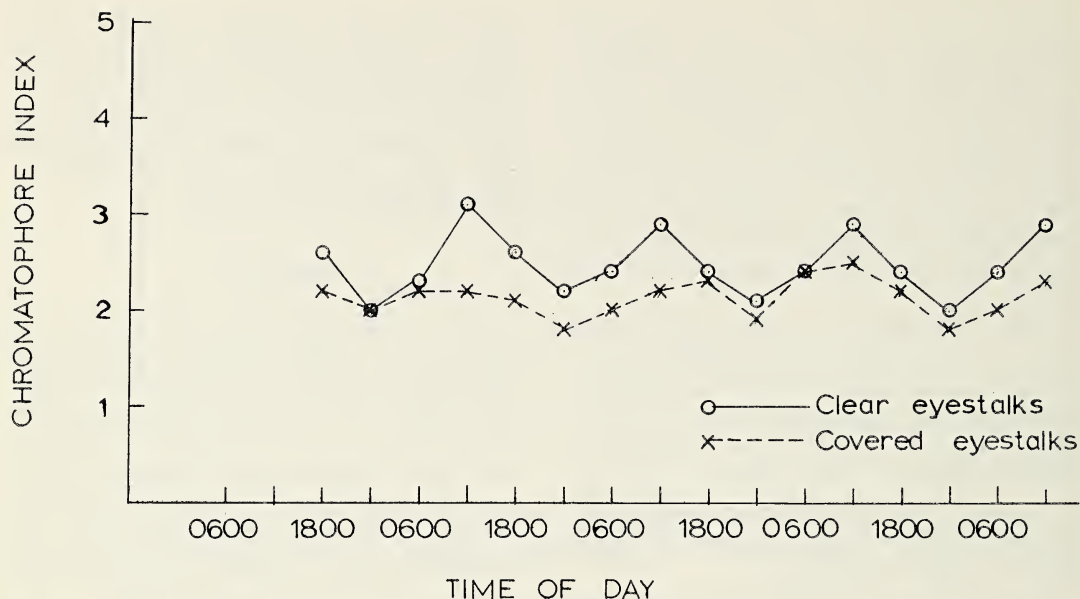
Fig. 6. The average daily indices of the darkly pigmented chromatophores in medium-sized *Ocypode cera-tophthalma* when the crabs were maintained in the normal photoperiod on white sand for 4 days with eyestalks covered with clear or red nail polish.

the chromatophores concentrates at night (Parker, 1948:51). On white sand this concentration of pigment at night enabled the crabs to blend with the white background. On black sand there was less blanching at night. This definite change in the normal pattern of chromatophore responses would indicate that the responses are flexible and are influenced not only by the light intensity but by the color of the background as well.

Smith (1938:252) observed in *Ligia* that a sudden change in the color of the background was frequently accompanied by a chromatophore response in which the animal gradually adapted to the new background color. Studies on *Uca* (Brown and Sandeen, 1948:366) showed a greater dispersion of dark pigment in animals on a dark background than on a light background when light intensity was the same.

Constant laboratory conditions were used for the reversed photoperiod experiments. The chromatophore rhythm which was established corresponded to the artificial night and day, with the animals being darkest during the artificial day and lightest during the artificial night, indicating that the rhythmic chromatophore changes can be reversed.

Brown (1961:510) reported that a daily rhythm of chromatophore responses will persist under conditions of constant darkness in many species. In the experiment reported here the results showed that a diurnal rhythm was maintained, although at a lower level on the Hogben and Slome scale when the crabs were maintained on white sand. The normal environment of these crabs is on white sand and in constant darkness, for they are active at night and spend the day underground. The conditions of the experiment conducted in total darkness were, therefore, quite similar to those of their natural surroundings. During the experimental period the crabs were very active, behaving as they normally do at night. Although the chromatophore rhythm was not destroyed under the conditions of constant darkness, it was evident toward the end of the last day that the pattern had started to decay. The crabs maintained in total darkness on black sand, however, showed very little change in pigment concentration with respect to time. Because the black sand is much coarser than the white, one must include the possibility that substrate characteristics other than reflectivity might influence chromatophore responses.

The observed daily chromatophore rhythm did not persist in the experiments in which the crabs were maintained in constant illumination. The light conditions of these experiments were completely foreign to the animals, and the crabs behaved sluggishly. There were no cues from the environment to aid in maintaining the rhythm, and it did not persist. There was no evidence of a persisting diurnal rhythm. The amount of illumination was the same for both groups of crabs, yet those on black sand showed a consistently greater degree of pigment dispersion, showing that there is a response to the color of the background.

In the final experiment an attempt was made to determine whether the observed daily responses were responses to a visual stimulus. Cowles (1905:23–24) reported that after painting the eyestalks of *Ocypode* with lampblack, no further color changes were observed. This observation, however, was not quantitative, for he observed only gross appearance and did not describe the condition of the chromatophores. In the present study the eyestalks of 10 medium crabs were covered with dark red nail polish. While it was uncertain whether this treatment blocked all the light transmission, the response suggested that the red coating effectively reduced visual reception. Normally the ghost crab demonstrates a shadow reflex, depressing its eyestalks when moved from the light into the shade or vice versa. The crabs whose eyestalks were painted with clear polish did demonstrate the reflex; the crabs whose eyestalks were painted red did not. The degree of pigment dispersion in the red-painted crabs was much less. Clear nail polish may have cut out some of the light, which might account for the decrease in amplitude of the daily chromatophore rhythm as compared with crabs with normal eyestalks. The results, however, suggest that the visual reception of light is an important factor in maintaining a daily rhythm of chromatophore changes.

SUMMARY

1. The Hawaiian ghost crab, when maintained on white sand, demonstrates a daily rhythm of chromatophore changes with maximum dispersion of dark pigment during the day and maximum concentration at night. On a black background the same daily rhythm of chromatophore changes is observed, but there is generally less concentration of pigment at all times.

2. In an artificially reversed photoperiod the crabs on both black and white backgrounds display a reversal of the daily rhythm of chromatophore changes.

3. In constant darkness crabs on white sand still display the daily rhythm but at a lower over-all level of pigment dispersion; on black sand the rhythm becomes irregular in constant darkness.

4. Under conditions of constant illumination crabs maintained on both backgrounds show little if any rhythm of chromatophore dispersion and concentration.

5. The observed chromatophore responses are primarily responses to visual stimuli, although in the absence of light evidence is given for an endogenous rhythm and for alteration of rhythm by substrate.

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Overt Responses of *Polychoerus carmelensis* (Turbellaria: Acoela) to Abrupt Changes in Ambient Water Temperature

ROBERT G. SCHWAB[1]

KNOWLEDGE of an animal's response to a change in the ambient environment contributes to an understanding of its behavior, activity pattern, and methods of survival. Responses to environmental stimuli by triploblastic animals having a comparatively low order of tissue/organ development as in the Acoela has special evolutionary significance because, according to the hypothesis of Hadzi, they are the stem group of the Eumetazoa and were derived from ciliates (de Beer, 1954; Hanson, 1958). Of special interest are the flatworms which inhabit tide pools of the midtide horizon, where ambient temperatures may fluctuate because of shallow, relatively nonturbulent water. Such is the habitat of the Acoela flatworm *Polychoerus carmelensis* in the vicinity of Monterey, California (Ricketts and Calvin, 1952). During low tide this species is often abundantly present on algae-covered rocks. At high tide *Polychoerus* takes shelter under rocks and gravel, apparently in response to water turbulence caused by the incoming tide. Because of potentially pronounced environmental changes within its ecosystem, *Polychoerus* was selected for study of the overt responses by an exothermic marine animal to changes in the ambient water temperature.

Dr. Donald P. Abbott, Assistant Director of the Hopkins Marine Station, contributed several much-appreciated suggestions during this study.

METHODS

Specimens of *P. carmelensis* collected at Point Pinos (vicinity of the Hopkins Marine Station of Stanford University, Pacific Grove, California) were transported to the University of California Animal Physiology Laboratory at Davis, California. One group of animals was maintained for 24 hr and another for 48 hr in a darkened chamber at a temperature of 13°–14°C. This temperature approximates that of Monterey Bay in late spring. In the following tests an individual flatworm was removed from the chamber, placed on a horizontal plastic grid, and quickly submerged to a depth of 1 cm in a controlled-temperature sea water bath. During the experiments the water temperature was maintained within ±0.5°C of the desired temperature at the upper surface of the submerged plastic grid. The amount of illumination from fluorescent room lights at water level was constant at 60 ft-c throughout all tests. This was sufficient to induce a photokinetic response from the dark-conditioned animals.

As an animal moved across the plastic grid, its horizontal movements during a 30-second period were transcribed by the author onto a record sheet grid. Such a record was obtained for each individual tested. All animals were allowed to travel a distance of about 1 cm before the record tracings were initiated. The total distance traveled, often in a highly erratic course, was measured from the record sheet grid; the rate of locomotion was computed in mm/min.

After being dark-conditioned for 24 hr, 10 individuals were tested at each of the following temperatures: 3°, 5°, 8°, 11°, 14°, 17°, 21°, 25°, 29°, 33°, 35°, and 38°C. No further tests were made on any individual, once its locomotion rate at a specific temperature was determined. On the following day, each test was repeated using 10 animals dark-conditioned for 48 hr. There was no apparent difference in the average rate of locomotion related to duration of conditioning. Therefore, the locomotion rate data for all 20 individuals tested at each specific temperature were consolidated.

RESPONSES TO AMBIENT WATER TEMPERATURE

Reactions to Cold Temperature

P. carmelensis placed in sea water at a temperature of 3°C immediately contracted into a U-shaped posture with normally ventral portion of the animal forming the inside surface of the U. Few animals exposed to this temperature had noticeable muscular or ciliary motion while in this posture. Thus, the well-developed automaticity normally associated with ciliary motion (Prosser and Brown, 1961) apparently did not occur in *P. carmelensis* exposed to sea water at 3°C. After several minutes' exposure, disintegration of the epidermal cells occurred, and shortly thereafter a gentle motion of the water caused by stirring with a probe resulted in disorganization of the body structure.

All *polychoerus* exposed to an ambient water temperature of 5°C contracted into the U-shaped posture and were motionless for several minutes. Thereafter most were capable of locomotion (it was necessary to test 24 individuals to obtain locomotion rates for 20 animals). These animals were motile long enough to measure locomotion rates ranging from 5.0 to 32.5 mm/min with an average of 17.4 mm/min. This was the lowest average obtained in these tests. At the same temperature, 16 individuals moved about while in the U-shaped posture. Apparently this movement was accomplished entirely by motion of cilia on the dorsal surface, since no muscular contractions were noticed as the animals glided over the surface of the plastic grid. These animals moved about for only a minute or two and thereafter tissue disintegration took place as described above. The highest rates of locomotion at 5°C were obtained from 4 animals that, after a short period in the U-shaped posture, moved in the typical flatworm posture. Within a few minutes movement ceased, whereupon they again contracted into the U-shaped posture and died.

Reactions to Changes in Ambient Water Temperature

The locomotion rate of *P. carmelensis* was clearly influenced by the temperature of ambient sea water under the conditions of these experiments. However, there were pronounced changes in the manner in which locomotion

occurred. Several of the 20 animals exposed to water at 8°C began to move while in the U-shaped posture. Locomotion was accomplished by action of the dorsal cilia, the only portion of the body in contact with the plastic grid. These animals soon reoriented to the typical flatworm posture and the rate of locomotion at 8°C was measured from this posture only. At this temperature *Polychoerus* traveled at an average rate of 44.9 mm/min. Accelerated locomotion rates associated with increases in ambient water temperatures were measured at 11°, 14°, and 17°C with average values of 64.8, 83.0, and 90.4 mm/min respectively. Thus, the average rate of locomotion for *P. carmelensis* acclimated at 13°–14°C increased from 17.4 to 90.4 mm/min in response to a 12-degree rise (from 5° to 17°C) in temperature. This increase in speed of locomotion took place at a nearly uniform rate of 6.1 mm/min/°C increase in water temperature (see Table 1).

P. carmelensis specimens respond to temperatures higher than 17°C by decreasing their rate of locomotion. A reduction in average locomotion rate was measured at 21°C (78.5 mm/min), 25°C (66.2 mm/min), 29°C (50.2 mm/min), and 33°C (32.8 mm/min). This results in a steady decrease in the speed of locomotion at an approximate rate of 4.4 mm/min/°C rise in temperature between 17° and 33°C.

Reactions to Warm Temperatures

At an ambient water temperature of 29°C *Polychoerus* usually contracted into a curled position with the posterior portion of the body drawn up under the more anterior portion. Locomotion in this posture was primarily accomplished by action of the anterior portion of the body, since much of the posterior portion was not in contact with the plastic grid. The animals had an average locomotion rate of 50.2 mm/min while in this posture and, although several animals died after 5–10 minutes' exposure, it is reasonable to assume that they would have found a more suitable temperature within this length of time in their natural habitat.

Most of the individuals exposed to an ambient water temperature of 33°C immediately contracted into the curled posture mentioned above and were capable of locomotion for only

TABLE 1

REACTIONS OF *P. carmelensis* TO CHANGES IN AMBIENT WATER TEMPERATURE*

TEMPERATURE (°C)	LOCOMOTION RATE (MM/MIN)		STANDARD DEVIATION	STANDARD ERROR OF THE MEAN
	Average	Range		
3**				
5	17.4	5.0– 32.5	6.83	1.51
8	44.9	25.0– 62.5	9.81	2.19
11	64.8	40.0– 90.0	14.21	3.18
14	83.0	62.5–115.0	14.70	3.25
17	90.4	57.5–122.5	17.06	3.82
21	78.5	45.0– 95.0	13.89	3.10
25	66.2	45.0– 87.5	11.40	2.53
29	50.2	35.0– 62.5	7.41	1.65
33	32.8	17.5– 65.0	11.49	2.57
35**				
38**				

* A total of 20 individuals was tested at each of the temperatures.
** See text.

1–3 minutes. Thereafter disintegration of the tissues took place. Some of the flatworms tested at this temperature immediately formed the U-shaped posture. After about a minute most individuals reoriented to the curled posture and moved about for a minute or two. After this short period of movement they again formed the U-shaped posture and all movement ceased. Animals removed after about 3 minutes' exposure to 33°C water temperature did not recover when placed in 14°C sea water. An exposure of 5–10 minutes at this temperature results in an apparently complete disorganization of the body structure.

Exposure to sea water at a temperature of 35°C resulted in a very brief but rapid locomotion by several of the 20 individuals tested. Generally this occurred while the animal was in the curled posture. However, most individuals remained in the U-shaped posture assumed immediately upon contact with the 35°C water and had no measurable amount of locomotion. All animals showed signs of tissue disintegration within 60 seconds after exposure.

Polychoerus exposed to sea water at 38°C appeared to die immediately. Several individuals were dipped into water at this temperature and then quickly returned to 14°C sea water but there were no recoveries.

DISCUSSION

The locomotion rate of *P. carmelensis* was clearly related to the water temperature under the conditions of these experiments. The nearly uniform increase of locomotion rate at 6.1 mm/min/°C rise in temperature between 5° and 17°C suggests that changes in tide pool temperatures may have a pronounced effect on the activity and behavior of this species. The mechanism by which temperature induces increased locomotion activity is not known. However, it is likely that this accelerated locomotion is fundamentally similar to the increases of chemical and physical reactions normally associated with an increase in temperature. Many biological processes, including rate of development, behavioral reactions, speed of locomotion, and metabolism show increases associated with higher temperatures (Prosser and Brown, 1961).

It is significant that the highest rate of locomotion occurred at a temperature (17°C) near that measured in these tide pools during late spring. This suggests that the maximum locomotion rate of *Polychoerus* may be a function of the most suitable ambient environmental temperature with respect to possible acclimatization of the animal.

The decrease in locomotion rate measured at ambient water temperatures above 17°C (4.4 mm/min/°C rise in temperature between 17° and 33°C) is considerably less than that measured for locomotion increases (6.1 mm/min/°C rise in temperature between 5° and 17°C). This suggests a temperature-related differential

response rate as well as a differential behavior response. The temperature threshold at which the type of response, increased or decreased locomotion, and the rate at which the response takes place is approximately 17°C for *P. carmelensis* accustomed to an ambient water temperature of 13°–14°C. A possible explanation for this is that accelerated locomotion results from a direct influence by the ambient temperature on body processes, and decreased locomotion results as a secondary effect of temperature-related factors, such as the reduced availability of oxygen as the ambient water temperature increases. *Polychoerus* obtains oxygen from the aquatic environment by diffusion through epidermal tissues. The physical characteristics of this species are such that sufficient oxygen for metabolic processes should be available from the environment at the higher temperature levels tested if the entire surface of the animal is effectively exposed to the environment. However, it is possible that little oxygen diffuses through the ventral epidermal tissues because of the close proximity of the animal to the surface on which it crawls. This would reduce by nearly one-half the effective diffusion surface and is a possible explanation for the curled position resulting from elevated temperatures in that this position exposes about one-half of the ventral epidermal tissue to the oxygen-bearing environment.

Locomotion of *P. carmelensis* at temperatures from 8° to 25°C inclusive takes place in the typical flatworm-type posture. The highest individual rate of locomotion obtained during these tests (2.08) was noted from a worm tested at 17°C. The lowest average locomotion rate in this temperature range was 0.75 at 8°C, and the highest average of 1.50 occurred at 17°C. These locomotion rates are expressed in mm/sec and were measured at a light intensity of 60 ft-c. They compare closely with the locomotion rates reported by Armitage (1961) of 0.86 mm/sec and 1.34 mm/sec measured at illumination levels of 6 and 37 ft-c, respectively. However, he states that the behavior of *Polychoerus* was highly erratic during his locomotion rate tests, in that some individuals spent considerable time turning the head from side to side and others ceased crawling before reaching the end of a 5-cm course. A possible explana-

tion of this erratic activity, based on the temperature-locomotion rate relationship obtained in my experiments, is that the water in the petri dish used by Armitage in his tests became warm during the course of the observations because of warm room temperature and/or heat from the light source used to stimulate locomotion. In the present tests, none of the 120 worms tested between 8° and 25°C showed such behavioral responses. However, several of those tested at 29°C and essentially all at 33°C reacted in the erratic manner described by Armitage.

Survival Value of Temperature-Locomotion Relationship

According to Armitage (1961), *P. carmelensis* does not possess a persistent diurnal rhythm. Therefore, this species must depend on an environmental "cue" or a combination of such environmental stimuli to regulate its daily activity pattern. Observations by Armitage indicate that light intensity and water turbulence play a pronounced role in the regulation of activity and behavior of this animal. Because of the pronounced influence on the velocity of movement resulting from slight changes in the ambient water temperature, it seems reasonable that temperature and temperature-related factors may also function as stimuli regulating activity and behavior.

Armitage postulates that on bright days the absence of *Polychoerus* from the upper surface of rocks and gravel during low tide and relatively calm water is caused by an increased negative phototropic response to high light intensity. However, on April 29, 1965, a cool but very bright day with morning sea water at about 15°C, I observed *Polychoerus* active on the upper surfaces of rocks and gravel throughout the period of low tide. This observation, made at the same location but earlier in the season than that by Armitage, documents the fact that high light intensity does not always cause a negative phototropic response, and suggests that there is more than a single factor regulating this behavior. Ambient water temperatures above 17°C cause a reduction in the rate of locomotion for animals conditioned to 13°–14°C. It is likely that this reduced rate of locomotion in response to such temperatures or

temperature-related factors corresponds to a less suitable ambient environment, and that such conditions in their natural environment may cause *P. carmelensis* to vacate the upper surfaces of rocks and gravel.

In my experiments *Polychoerus* specimens were totally incapacitated soon after exposure to ambient water temperatures above 29°C. It is reasonable to assume that environmental factors would trigger a behavioral escape mechanism should such temperatures occur in their natural habitat. The survival value of such an environmental stimulus or combination of stimuli is dependent upon the sensitivity and response of the animal to this factor or factors. Armitage reports a 55% increase in rate of crawling when the light intensity was increased 640%, and that in his tests *P. carmelensis* was negatively phototropic. Although the magnitude of the light intensity change (in ft-c or in percent increase) and the sensitivity of the animals in terms of response to this factor (rate of crawling in mm/sec or percent increase) cannot be directly compared to similar calculations with respect to temperature change and associated activity response, it seems certain that *Polychoerus* is at least as sensitive to ambient water temperature as it is to light intensity.

Costello and Costello (1938) indicate that *P. carmelensis* may be positively phototropic in that individuals showed a tendency to group on the moderately lighted side of an aquarium. Therefore, there is evidence of both positive and negative phototropic response for this species. Armitage suggested that this species may have a differential response to low and high light intensities. Whether such a light sensitivity threshold exists, or whether the behavioral evidence supporting this possibility results from a water temperature–light intensity relationship, is at present unknown.

The physical properties of water are such that the heat energy associated with even relatively high light intensities may have little immediate effect on the temperature of the tide pool. Conversely, tide pool temperatures may in time become elevated on overcast days with relatively low light intensities. Thus, it is possible that the absence of this species from tide pools on bright days as observed by Armitage may be at least in part the result of an elevated ambient

water temperature associated with high insolation, rather than the result of high illumination levels as a discrete factor. Regardless of the nature of causative stimuli, the rate of locomotion between 8° and 29°C is sufficient for *Polychoerus* to seek a more desirable situation under rocks and gravel should the tide pool environment warrant such behavior.

Environment-Induced Posture Responses

The U-shaped posture resulting from low, high, and often from moderately high ambient water temperatures appears to be the same posture described by Armitage for *Polychoerus* exposed to osmotically unsuitable salinity concentrations. Apparently this species has only the U-shaped posture response to both hypo- and hypertonic sea water, since Armitage does not mention other postures such as the curled posture observed in my experiments at certain elevated water temperatures.

During my experiments the U-shaped posture often occurred as a response to a gentle mechanical stimulus from contact with a soft-bristled brush used to transfer the animals from one container to another. The fact that this posture occurs as a result of temperature change, salinity change, and mechanical stimulus suggests that this posture is a characteristic behavior response to many undesirable environmental conditions.

Further experimentation may show that the curled posture also occurs as a response to a variety of stimuli. However, it is certain that this response is clearly associated with ambient water temperatures near the upper lethal level. It is not known if the curled-posture response occurs as a direct result of temperature perception by a discrete thermoreceptive mechanism or as a characteristic response to temperature-related environmental factors. It may be that the curled posture common at 29°C functions to increase the amount of surface area in direct contact with the aquatic environment, thus facilitating gaseous exchange, while enabling the animal to take shelter. The U-shaped posture exposes even more surface area but has no obvious survival value at temperatures above 29°C, inasmuch as the locomotion rate is low and the animal soon dies. However, this conclusion is hypothetical, since possible advan-

tages of either posture to animals exposed to high water temperatures are not known.

CONCLUSIONS

1. The ambient water temperature clearly influences both the rate and the sign of *Polychoerus'* locomotion. A rate-directional response threshold was measured at 17°C for animals conditioned to 14°C in that, as temperatures increased from 5° to 17°, the speed of locomotion increased from an average of 17.4 to 90.4 mm/min, at the rate of 6.1 mm/min/°C. Further temperature increases from 17° to 33°C caused a steady decrease in locomotion speed from an average of 90.4 to 32.8 mm/min, and the rate of reduction per degree of temperature increase, − 4.4 mm/min, was relatively low.

2. The highest average speed of locomotion (90.4 mm/min) and the greatest individual rate (122.5 mm/min) were measured at 17°C, which is near the temperature of sea water at the location and season at which these experiments were conducted. This suggests the possibility that the maximum locomotion rate is a function of the ambient water temperature with respect to possible seasonal acclimatization by the animal.

3. It is postulated that the increased rate of locomotion as temperatures changed from 5° to 17°C corresponds to a general temperature-related acceleration of the body processes. It is not known why temperature increases above 17°C cause a reduction of locomotion speed. Possibly this is a function of decreased amounts of available oxygen due to elevated water 'temperatures and/or crossing a critical temperature threshold for enzymatic action.

4. *Polychoerus* has a differential movement posture with respect to high and low water temperatures. At 5°C this species contracts into a U-shaped position, and movement at an average rate of 17.4 mm/min results from motion of the cilia on the dorsal surface of the animal. In ambient sea water temperatures of 29°C and

above, movement generally occurs while the animal is in the usual flatworm position, but with the posterior portion of the body drawn up under the more anterior portion. In this position the average rate of movement was 50.2 mm/min at 29°C and 32.8 mm/min at 33°C.

5. Sea water temperatures slightly below 5°C and above 29°C are not suitable for the survival of *P. carmelensis* conditioned at a temperature of about 14°C. However, the rate of locomotion at these temperatures appears sufficient to allow this species to avoid such conditions should they occur in the tide pool. Measurements of temperatures prevailing beneath the rocks and gravel in these tide pools is needed.

6. It is probable that the temperature of the ambient sea water, as well as the intensity of illumination and the turbulence of water, function as an environmental stimulus regulating the activity and behavior of *Polychoerus*.

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The Osteology of the Congrid Eel *Gorgasia punctata* and the Relationships of the Heterocongrinae[1]

RICHARD H. ROSENBLATT[2]

ABSTRACT: The osteology of *Gorgasia punctata* is described, figured, and compared with that of other congrids. *Gorgasia* is clearly referable to the subfamily Heterocongrinae. The heterocongrines agree with the Congridae in several important features, and do not differ in fundamental respects. Therefore, the group is recognized as a subfamily of the Congridae. *Gorgasia* is the most primitive heterocongrine, and agrees with the anagoine congrids in having a lateral ethmoid process. Because of this and other similarities it is suggested that the Anagoinae and Heterocongrinae arose from a common stem. The genus *Xarifania* was erected on the erroneous basis of lack of caudal rays. It is synonymized with *Taenioconger*.

THE CONGRID EEL *Gorgasia punctata* was placed by its describers in the little known apodal family Derichthyidae (Meek and Hildebrand, 1923). Böhlke (1951) was the first to point out that the affinities of *Gorgasia* were with *Heteroconger*. Gosline (1952) provisionally placed *Heteroconger* and *Gorgasia* in the Congridae. Böhlke (1957) described the osteology of the related *Nystactichthys halis* and placed the eels allied to *Heteroconger* in the Congridae, but considered them to constitute the distinct subfamily Heterocongrinae.

Böhlke considered *Gorgasia* to be the most primitive genus of the Heterocongrinae on the basis of its more complete complement of head pores, its uncoalesced upper labial flanges (called by him the "free edge of lip"), a well-developed pectoral fin, and its unspecialized maxillary dentition. He considered *Gorgasia* to be specialized, however, in that the caudal rays are much reduced and covered by thick skin. Internal characters were not considered, since the only complete specimen then available was the holotype.

Recent collections made by personnel of the Scripps Institution of Oceanography have amassed rich material of several species of eastern Pacific heterocongrines, including *Gorgasia punctata*. Because of previous uncertainties regarding the exact position of *Gorgasia* in eel classification, a study of the osteology of this species seemed worthwhile.

ACKNOWLEDGMENTS

MATERIALS AND METHODS

The two adults of *Gorgasia punctata* were taken from a series of 69 (SIO62-720-26A, Bahía Magdalena, Baja California, Mexico). These were bone-stained with alizarin and cleared in glycerine. The neurocranium was dissected out of one specimen, and the drawings were made from the dried preparation. In addition I have utilized single-stained and cleared specimens of *Taenioconger digueti* Chabanaud (SIO65-278, Gulf of California), *T. herrei* Wade (SIO61-261, Gulf of California), *T. hassi*[3] (Klausewitz and Eibl-Eibesfeldt)

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[3] *Taenioconger hassi* was originally described in the genus *Xarifania*, of which it is the type species

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(unnumbered, D'Arros Island, Amirantes Islands), *T.* n.sp. (SIO62-42, Bahía Banderas, Mexico), and *Ariosoma gilberti* (Ogilby) (SIO62-77, Sinaloa, Mexico).

OSTEOLOGY

NEUROCRANIUM (Fig. 1): The skull is truncated posteriorly, except where the exoccipital flanges break the outline. The premaxillaries, ethmoid, and vomer are fused, with no suggestion of articulations, such as were reported by Böhlke (1957) for *Nystactichthys halis.* The anterior, triangular tooth-patch may represent the premaxillary dentition. The dorsal or ethmoid portion of the complex is very thin, and is reduced medially to a septum, so that it is shaped much like an I-beam in cross section. Laterally the ethmoid portion is expanded, and gives rise to two heavy, forward-curving processes. These are very similar to the "lateral ethmoid processes" reported by Asano (1962) for *Anago* and *Alloconger.* Below this are two small projections from the lateral face of the vomer. These vomerine processes are difficult to distinguish from the base of the lateral ethmoid process. They are more evident in *Taenioconger* and, judging from Böhlke's figures 3B and 3C, are developed in *Nystactichthys* as well. Posteriorly on the under side of the cranium, parts of the prootic and basioccipital are expanded to form a prominent auditory bulla, which contains a large otolith (presumably the sagitta). The foramen magnum is surrounded by exoccipital flanges, which grasp the first vertebra. The supraoccipital is well developed, but does not completely separate the epiotics, which are in contact posteriorly. The parietals are sutured in the specimen figured,

(Klausewitz and Eibl-Eibesfeldt, 1959). The sole distinction of the genus *Xarifania* was the supposed lack of caudal rays. The tail-tip of *X. hassi* is fleshy but flexible and clearly contains well-developed caudal rays. These are visible under direct light and are obvious when transmitted light is used. In addition to the Amirantes specimen, I have examined a paratype of *X. hassi* (ANSP 94706) through the courtesy of J. Böhlke. I can find no other important differences, either in external morphology or osteology, between *X. hassi* and the species of *Taenioconger* examined. The nominal genus *Xarifania* is considered, therefore, to be a synonym of *Taenioconger.*

FIG. 1. Head skeleton of *Gorgasia punctata*. *A,* Lateral view, including pectoral girdle; *B,* neurocranium, lateral view; *C,* neurocranium, top view; *D,* neurocranium, bottom view. *AA,* Articular angular; *BO,* basioccipital; *BR,* branchiostegal ray; *CL,* cleithrum; *CO,* circumorbital; *D,* dentary; *EO,* exoccipital; *EP,* epiotic; *FR,* frontal; *HMD,* hyomandibular; *HOC,* hypocoracoid; *HRC,* hypercoracoid; *IOP,* interopercle; *LEP,* lateral ethmoid process; *MX,* maxillary; *N,* nasal; *OBS,* orbitosphenoid; *OP,* opercle; *PAR,* parietal; *PAS,* parasphenoid; *PEV,* premaxillary ethmovomerine block; *POP,* preopercle; *PP,* palatopterygoid; *PR,* pectoral ray; *PRO,* prootic; *PT,* pterygiophore; *PTO,* pterotic; *PTS,* pterosphenoid; *QU,* quadrate; *SCL,* supracleithrum; *SO,* supraoccipital; *SOP,* subopercle; *SPO,* sphenotic.

but in another they are fused for the anterior one-quarter of their lengths. The frontals are completely fused, with no sign of a suture or median ridge. There are well-developed canals along the lateral margins of the pterotics and frontals, with two large foramina anteriorly, but there is no transverse canal across the frontals.

SUSPENSORIUM AND JAWS (Fig. 1): As

might be expected from the short oblique mouth, the suspensorium is strongly inclined forward. The hyomandibular and quadrate are massive. The palatopterygoid is developed as a broad lamina, which is attached by a ligament to the vomer. The maxillary contacts the neurocranium at the tip of the snout. The posterior end of the maxillary is expanded, but the remainder is a narrow lamina. There is no pedicel anteriorly.

OPERCULAR SERIES (Fig. 1): The well-developed opercular bones are strongly ossified. The preopercle is triangular, like that of *Taenioconger*, but unlike that of *Nystactichthys* as illustrated by Böhlke (1957). The blocky and subtriangular interopercle has a pronounced anterior extension. The crescentic subopercle curves upward under the lower angle of the opercle. The dorsal margin of the broadly crescentic opercle is deeply concave; its upper-rear corner is far above the upper end of the hyomandibular.

HYOID ARCH (Fig. 2): This arch consists of the unpaired glossohyal and urohyal, and paired upper hypohyal, ceratohyal, and epihyal. The interhyal is absent. All the branchiostegal rays are inserted on the lateral surfaces of the arch, one on the ceratohyal and seven on the epihyal. In *Nystactichthys* and *Taenioconger*, in contrast, two branchiostegals are inserted on the ceratohyal. The urohyal is needle-like, with an expanded and flattened anterior end. The dorsal surface of the glossohyal is grooved.

SHOULDER GIRDLE (Fig. 1): The cleithrum and supracleithrum are well developed. The expanded head of the supracleithrum is bifurcate in the specimen illustrated, but not in another. The well-ossified hypercoracoid and hypocoracoid are connected by cartilage. The four hourglass-shaped actinosts are small, but well ossified. According to Böhlke *Nystactichthys* has no actinosts, but the species of *Taenioconger* that I have examined are like *Gorgasia* in this respect.

VERTEBRAE AND ASSOCIATED BONES (Fig. 3): In one specimen the vertebrae number 144, of which 45 precede the anus. Figure 3A represents a cross section at the level of the 17th vertebra; Figure 3B illustrates the 17th to 19th vertebrae in lateral view. The vertebrae anterior to the dorsal origin bear well-developed, crest-like neural spines. The remainder of the abdominal vertebrae have large neural arches, but
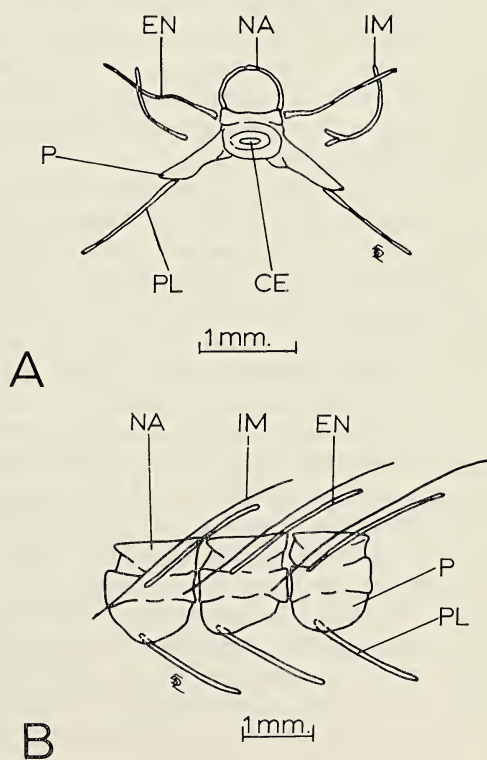

A

B

FIG. 2. Hyoid apparatus of *Gorgasia punctata* from below. *BR*, Branchiostegal ray; *CH*, ceratohyal; *EH*, epihyal; *GH*, glossohyal; *HH*, hypohyal; *UH*, urohyal.

FIG. 3. Vertebrae and associated bones of *Gorgasia punctata*: A, Front view of 17th vertebra; B, side view of 17th to 19th vertebrae. *CE*, Centrum; *EN*, epicentral; *IM*, intermuscular; *NA*, neural arch; *P*, parapophysis; *PL*, pleural rib.

no neural spines. The first 4 vertebrae bear strongly-developed, winglike transverse processes. These curve out and back, and each has on its posterior margin a long, thin, backward-directed process that seems to represent a fused epicentral (these structures lie on the same plane as the epicentrals associated with the more posterior vertebrae; furthermore, epicentrals are otherwise lacking on the first 4 vertebrae). The 5th through 9th vertebrae bear epicentrals, and weak transverse processes without backward prolongations. Böhlke mentioned no such peculiar condition in *Nystactichthys halis,* nor can I find transverse processes on the anterior vertebrae in *Taenioconger digueti* or *T. herri.* In *T. hassi,* however, weak transverse processes are developed on the first few vertebrae. In *Gorgasia* the transverse processes are more weakly developed posterior to the 4th vertebra, and are not noticeable posterior to the 10th vertebra.

The abdominal vertebrae bear strong parapophyses to which, posterior to the 6th vertebra, are articulated strong pleural ribs. There is a strong median vertical ridge on each parapophysis. The first haemal spine appears 15 vertebrae behind the anal origin, and the pleural ribs are present to this point.

The caudal vertebrae bear transverse processes, commencing 6 vertebrae behind the anal origin. The transverse processes regress toward the tail-tip and are no longer apparent on the 10th vertebra before the caudal. The neural arches of the caudal vertebrae are smooth until about the 60th postanal vertebra, which bears the first neural spine, in the form of a small projection. The neural spines persist as low conical projections until 17 vertebrae from the tail-tip, behind which they become increasingly higher and more bladelike until they assume the shape shown in Figure 3. The haemal spines are also small and inconspicuous anterior to the 17th vertebra from the tail-tip. Thereafter, like the neural spines, they become increasingly higher and more bladelike. Shortly before the tail-tip the haemal spines become divided, so that the haemal arches are again open, as on the precaudal vertebrae (Fig. 4).

Epicentrals are associated with all vertebrae except the last 10. Epipleurals appear 6 vertebrae behind the anus and persist until 15 vertebrae before the tail-tip.
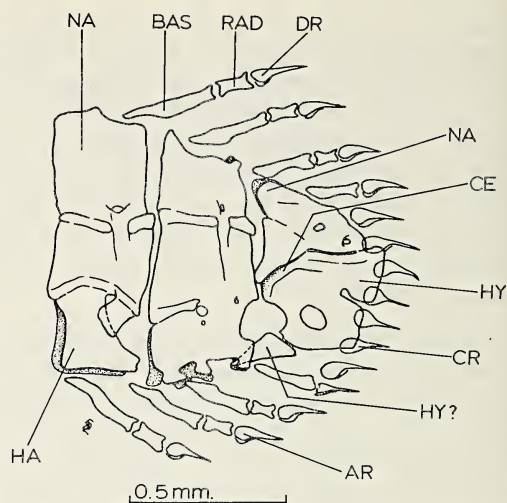

FIG. 4. Last 3 vertebrae of *Gorgasia punctata,* lateral view. *AR,* Anal ray; *CE,* centrum; *BAS,* basal element of pterygiophore; *CR,* caudal ray; *DR,* dorsal ray; *HY,* hypural; *NA,* neural arch; *RAD,* radial element of pterygiophore.

Dorsal and ventral intramuscular bones are well developed, and associated with all but the first 12 and last 4 vertebrae. Most of the intramusculars are simple; one of those illustrated in Figure 3 happens to be bifurcate.

CAUDAL AND ASSOCIATED STRUCTURES (Fig. 4): The tail-tip of *Gorgasia* is hard and pointed, with the fin rays concealed. However, the caudal skeleton is well developed and complex. As mentioned above, the neural and haemal arches and associated spines become expanded posteriorly, and the haemal and, to a lesser extent, the neural arches become open. According to the terminology of Nybelin (1963), there is but one ural centrum. Fused to it is a large hypural plate, probably consisting of several fused hypurals. The structure labeled HY? in Figure 4 is somewhat problematical. It has a basal-less fin ray associated with it and thus might be termed a hypural, but from its position it is difficult to determine whether it is itself associated with the last preural centrum or the ural centrum. Likewise, the nature of the dorsal element labeled NA is somewhat ambiguous. It might be termed an epural, but since it is fused to the centrum, and divided anteriorly like the preceding neural arch, I term it a neural arch, despite the circumstance that it bears two "prin-

cipal" caudal rays. A strong process curves forward and downward from the neural arch element. It probably serves as a muscle attachment and may be associated with tail-first digging in sand. An essentially similar caudal skeleton has been figured by Böhlke for *Nystactichthys halis,* and I have found the caudal skeleton of *Taenioconger digueti, T. herrei, T. hassi,* and *T.* n.sp. to be basically the same.

CIRCUMORBITALS AND LATERAL LINE CANALS: The circumorbital ring is complete, consisting of at least five weakly-ossified and roofless bones. Apparently the small "supraorbital" illustrated by Asano (1962) for several Japanese congrids is absent. The temporal canal is encased in bone in *G. punctata* only, among the species examined. The lateral-line canal along the body is contained in a series of ossicles (lateral-line scales?). Anteriorly these are developed as unconnected but closely opposed tubes, which posteriorly gradually become less strongly ossified, so that along the midbody there is an open trough consisting of a series of ossified half-rings. In the species of *Taenioconger* examined, the lateral-line ossicles are developed as short, widely-spaced, troughlike ossifications.

RELATIONSHIPS OF THE HETEROCONGRINAE

The heterocongrines resemble the Ophichthidae in several respects. In both groups the ribs are laminar, and the neural spines reduced (vestigial in the ophichthids), as are the circumorbitals. In *Gorgasia* and in some species of *Taenioconger* the caudal fin is short and the tail-tip fleshy. In all, the body is elongate and circular in cross section. The pectoral fin, as in many ophichthids, is reduced (varying from small in *Gorgasia* to minute in *Nystactichthys* and *Taenioconger* to absent in *Heteroconger*). In addition to these structural characters, both groups share the sand-dwelling habit. However, the characters given by Gosline (1951) to separate the Congridae and the Ophichthidae (except that it is now known that many congrids have an auditory bulla) serve to distinguish *Gorgasia* and its allies from the ophichthids as well. In addition, it may be noted that the Congridae have the parapophyses divided by a vertical ridge and have a vomerine process,

to which the palatopterygoid is ligamentously attached—features that appear to be lacking in the Ophichthidae.

The superficial similarities between *Gorgasia* and the ophichthids are certainly parallel adaptations to a similar mode of life, and the minor osteological similarities may be adaptations as well.

Although recognizing the close relationship between the two groups, Klausewitz and Eibl-Eibesfeldt (1959) maintained the family Heterocongridae as distinct from the Congridae. Their action was based on behavioral differences and on bone reduction and "Fensterbildung" (fenestration?) in the skeleton. However, their illustration of the head skeleton of *Xarifania h. hassi* shows a well-developed skull and well-integrated jaws, suspensorium, and opercular series. On the basis of the present investigation there are no grounds (except that the circumorbital series is less well developed) for the contention that the skeleton has undergone important reduction in comparison with that of the Congridae.

There is, in fact, nothing in the osteology of the heterocongrines I have examined that would preclude the inclusion of the group in the Congridae. The heterocongrines possess the basic congrid characters of ankylosed frontals, forward-inclined suspensorium, few and nonoverlapping branchiostegals, maxillary-ethmoid articulation near tip of snout, caudal vertebrae with transverse processes, skull truncate posteriorly, parapophyses divided by a vertical ridge, and a lateral process on the vomer.

The chief osteological differences are: neural spines absent on most abdominal vertebrae (and on most caudal vertebrae as well in *Gorgasia*); neural and haemal arches becoming high and bladelike near the tail-tip; urostylar vertebra better developed, and supporting structure of caudal more complex; epineurals and epipleurals lost 10–15 vertebrae before tail-tip; circumorbital series reduced and less ossified. Stronger divergences from the basic congrid type are found in nonosteological characters. In most of the Congridae the muzzle is elongate, and the olfactory organ is well developed, with numerous lamellae. In the heterocongrines the muzzle is short, the eye is relatively large, and the olfactory rosette is much smaller, with

few lamellae (ca. 20). This distinction is no doubt correlated with a change in food habits (Klausewitz and Eibl-Eibesfeldt, 1959). Also the habit of living colonially in sand tubes is unknown in other congrids.

These differences and similarities seem to bear out Böhlke's (1957) contention that the Heterocongrinae should be regarded as a well-defined subfamily within the Congridae. That there are profound differences in behavior and ecology is undoubted, but these have not involved any fundamental changes in the basic congrid body plan.

Until recently, little information has been available on the osteology of the family Congridae. However, Asano (1962) has presented detailed information on the anatomy of 10 genera and 14 species of Japanese congrids. On the basis of his study, Asano recognized two subfamilies, the Anagoinae and the Congrinae (the Heterocongrinae were not considered). The Anagoinae were said to differ from the Congrinae in that there is a forward and laterally directed process on the ethmoid, the supraoccipital is absent, there are only four suborbitals, the abdominal and caudal vertebrae are about equal in number, the gas bladder is attached to the parapophyses, the tail-tip is hard, the caudal rays are short, the fin rays are unsegmented, and the lateral-line scales are well developed.

Asano assigned two genera, *Anago* and *Alloconger*, to the Anagoinae. I can confirm that *Ariosoma* belongs here, as does the recently described *Paraconger* Kanazawa 1961.

The heterocongrines share characters with both the Anagoinae and the Congrinae. They agree with the congrines in that the supraoccipital is present, there are many more caudal than abdominal vertebrae, and the gas bladder is free from the parapophyses. They agree with the anagoines in that the fin rays are unsegmented, the caudal is reduced, and the lateral-line scales are well ossified (corresponding to Asano's "*Anago* type"). I have been unable to determine with certainty the number of suborbitals in the heterocongrines.

Gorgasia alone agrees with the Anagoinae in having a lateral ethmoid process. In this connection it is important to establish the evolutionary position of *Gorgasia*. Böhlke (1957)

gave reasons for considering *Gorgasia* to be in most respects the most primitive of the Heterocongrinae. His conclusions are borne out in this study, except for the discovery in *Gorgasia* of peculiar, expanded transverse processes on the anterior vertebrae, and the loss of an anterior maxillary pedicel. These specializations probably preclude *Gorgasia* as an ancestor, but they do not militate against the hypothesis that *Gorgasia* is more generalized over-all, and probably was an earlier offshoot of the heterocongrine line.

The retention in *Gorgasia* of a lateral ethmoid process indicates relationship with the anagoine line. It seems unlikely that the agreement represents convergence. Eels have evolved a number of structures bracing the maxillary, correlated with elongation of the gape and with the use of the jaws in biting and crushing (Gosline, 1951; Asano, 1962). However, the trend in heterocongrine evolution has been in the other direction, toward shortening of the gape and development of a jaw structure and dentition suitable for snapping at planktonic prey. It may be that the retention of the lateral ethmoid process in *Gorgasia* has allowed the loss of the maxillary pedicel.

It seems plausible to hypothesize that the Heterocongrinae and Anagoinae arose from a common ancestor which had a lateral ethmoid process, a supraoccipital, unsegmented fin rays, and well-developed lateral-line scales. It seems likely that the sand-burrowing habit (known for *Anago*) had already been developed. The two groups have diverged sharply, however. The development of the plankton-feeding habit in the heterocongrines has been accompanied by important changes in the head. The mouth has become short and oblique, and the dentition specialized. The development of a short oblique mouth as an adaptation to snapping at plankton or small prey has taken place in a number of fishes. Compare, for example, the serranid genus *Epinephelus*, which feeds on relatively large prey, with the plankton-feeding *Paranthias*. A similar phenomenon can be seen if the bottom-feeding embiotocid genus *Micrometrus* is compared with the closely related genus *Brachyistius*, which feeds in midwater (Hubbs and Hubbs, 1954). Walter A. Starck II has pointed out to me that the shortening of the

muzzle in these fishes results in the placement of the eye close to the tip of the snout, and thus allows for close-up binocular vision. Thus, vision has become more important in prey finding in heterocongrines, and the eye is much enlarged and the olfactory organ much reduced. The lateral-line system on the head has likewise become reduced, again probably correlated with the increased dependence on vision. The great elongation of the slender body would seem to be an adaptation to getting the head well off the bottom, and yet maintaining contact with the sand tube which is used for cover. (The normal posture of a heterocongrine is vertical, with the anterior one-half to two-thirds of the body out of the sand tube.)

On the other hand, the anagoines, except in the loss of the supraoccipital, have diverged much less from the basic congrid type, either in structure or in behavior.

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The Flora of Romonum Island, Truk Lagoon, Caroline Islands

Benjamin C. Stone[1]

Romonum Island (7° 25′ N, 151° 40′ W) is one of the smaller central islands in Truk, a large island complex comprising several peaks of volcanic origin within a large atoll-like reef. Hence sometimes Truk is called an "almost-atoll," because it is in a transitional stage between younger islands, such as Ponape or Kusaie, and older atolls, such as those of the Marshall Islands group. Romonum itself is relatively small and low, nearly a mile in length and half a mile in width, with a rounded hill at the eastern end rising to a height of 167 ft, with fairly steep sides on the east and northeast, and flat or gently sloping land to the west and south. Two extensive swamps occur, one toward the western end and another larger one toward the eastern end, both on the south side of the island. A sandy beach occurs along the southwestern tip and at several other localities on the western and southern coasts, while ramparts of black basalt boulders occur at several localities around the perimeter, especially on the east end.

The island is situated slightly northeast about 4 miles from Tol Island (Truk's largest and highest island), and about 2.9 miles due north of Fala-beguets I. (using the name shown on the 1944 edition Hydrographic Office map), and about 2.4 miles slightly northwest of Udot I. Moen Island, location of the U.S. Trust Territory Truk District Headquarters, is nearly 12 miles to the northeast.

As is true of virtually all of the islands within the encircling reef (excluding the coralline reef islets), Romonum is of volcanic origin. Except for the well-developed sandy beach, the island is composed of black basalt; no high raised limestones are found here or anywhere in Truk (although a few terraces scarcely a meter high do occur). The geological history of Truk is complex: the islands are much sunken or eroded; there are drowned valleys, wave-cut terraces (at about 40 m alt. and again

at 100 m alt.), and other evidences of both subsidence and emersion. However, little of this is in sight in Romonum. For a fuller geological account, publications by Tayama (1940), Hess (1946), Bridge (1948), and, for a brief description, Gressitt (1954) may be consulted.

In January 1965, I was enabled to visit both Truk and Ponape (as well as Saipan and Rota) through the generosity of the Trust Territory Government. At that time Prof. Ward Goodenough of the Department of Anthropology, University of Pennsylvania, was engaged in a lengthy restudy of the people of Romonum Island, and he invited me to stay for a time there. This invitation led to a sojourn of several days, from January 28 to 31. During this time a collection of plants was made, and most parts of the little island were visited, with the help of Oliver Goodenough as guide. Dr. Goodenough has allowed me to make use of his map, to which I have added some indications of the vegetation (Fig. 1). He has also provided his critical ear, a knowledge of Trukese dialects, and the orthography for most of the plant names given herein. Most names were verified by Dr. Goodenough; other names are in the form shown in P. J. R. Hill's mimeographed list of Trukese plant names, or are approximations in my own spelling.

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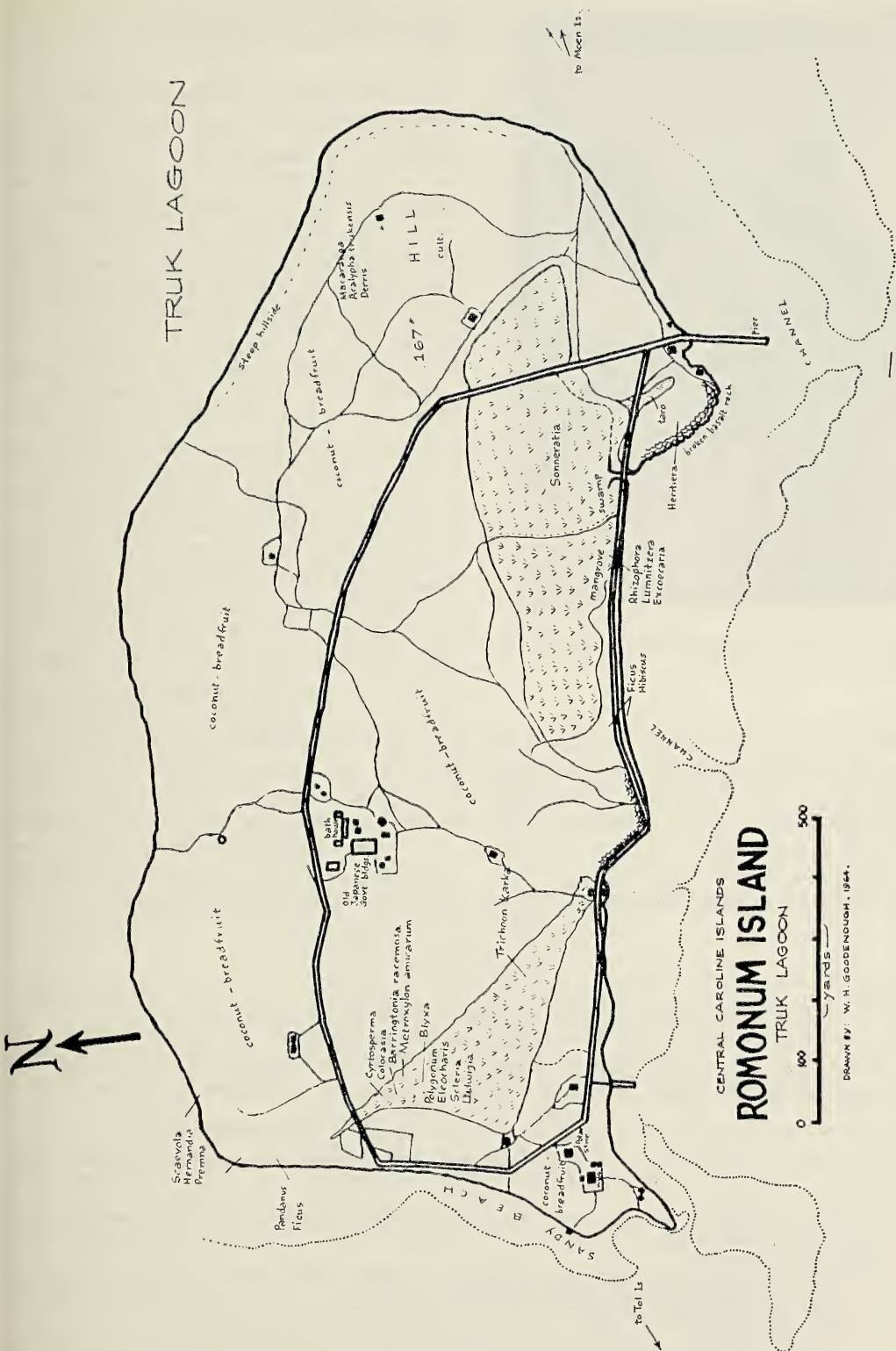
FIG. 1. Map of Romonum Island (courtesy of W. H. Goodenough). Characteristic plant species are indicated. Distances, outline, and details should be considered as approximations.

FIG. 1. Romonum Is.

FIG. 2. Prof. W. H. Goodenough, during his lengthy visit on Romonum.

was helpful in many ways. Prof. W. H. Goodenough and Mrs. Goodenough provided house and sustenance on Romonum, and Oliver Goodenough acted as guide. Finally, I must thank the College of Guam and especially Dr. A. C. Yamashita for the opportunity and support provided for the work undertaken on this

trip; and thanks are also due to the many other friends who were of assistance.

THE FLORA OF ROMONUM ISLAND

The following key and species list is undoubtedly not complete, but it includes the most common species of vascular plants on Romonum. There are probably additional species on the northeastern part of the island, which I did not cover thoroughly; and no doubt some weeds and cultivated plants were missed, or will be introduced in the future; still, the species cited here represent, I believe, the bulk of the island's vegetation. A key to species is provided, but of course it can only account for the species listed, and additional discoveries will have to be added. A number of plants are absent or represented very sparsely; *Messerschmidia*, for example, common on atolls and limestone areas of other islands, was not found; *Pemphis* was seen only once, and as an isolated individual; *Ipomoea pes-caprae* was not found, but may well occur on the north beach (its common associates, such as *Canavalia maritima, Wedelia biflora,* and *Scaevola* were found); *Polyscias grandifolia, Soulamea amara, Suriana, Pisonia grandis,* and other representative atoll species, found elsewhere in Truk, did not appear. In this respect Romonum resembles Yanagi Islet, only a few miles away in Truk Lagoon, the vegetation of which was described a few years ago (Hill and Stone, 1961), and which interestingly is also deficient in species typically associated with coral atolls.

KEY TO SPECIES

Only the vascular plants are accounted for here; for bryophytes the reader is referred to Miller, Whittier, and Bonner (1963); for marine algae to Okamura (1915) and Taylor (1950); for other groups there is no comprehensive treatment for Truk, but papers on lichens and fungi have been written by Imazeki (1941), Kobayasi (1939), Jatta (1903), and Sydow and Sydow (1921).

I. Flowerless plants bearing spores in sporangia, these usually borne on the backs or edges of fronds (Ferns)
  1. Fronds simple, to several feet long, forming a large nest or rosette; epiphytes; sori (groups of sporangia) oblique, linear .... *Asplenium nidus*
  1. Fronds lobed or divided
    2. Sporangia covering the entire lower surface of the leaflets; fronds to several feet long, leathery, somewhat dimorphic; 1-pinnate; swamp ferns .... *Acrostichum aureum*
    2. Sporangia in groups (sori)
      3. Fronds deeply parted, the lobes entire; sori sunken in pits, these evident on the upper surface as bumps; terrestrial or epiphytic ferns with creeping rhizomes .... *Phymatodes scolopendria*
      3. Fronds pinnate or bi- or tripinnate
        4. Fronds 1-pinnate
          5. Sori kidney-shaped; lobes of pinnae crenate .... *Nephrolepis*

        5. Sori round; lobes of pinnae acute .... *Cyclosorus*
    4. Fronds bi- or tripinnate, deltoid in outline .... *Davallia*

II. Flowering plants
  1. Monocotyledons (seed with 1 cotyledon; leaves usually with parallel venation; root system fibrous or without a tap-root; woody species with numerous discrete fibres traversing a softer tissue; flower parts frequently in 3's or multiples of 3)
    2. Trees or large woody shrubs
      3. Palms; trunks large, unbranched, erect, or in *Nypa* submerged, ± horizontal, with terminal crown of large pinnate leaves
        4. Stems horizontal, submerged in swamps .... *Nypa*
        4. Stems erect
          5. Fruits ovoid, smooth, large (to 12 inches diameter or more), edible (coconuts) .... *Cocos nucifera*
          5. Fruits smaller, subglobose, covered closely by glossy brown overlapping scales, inedible .... *Metroxylon*
      3. Trunks branching, leaves not divided
        6. Leaves elongate, toothed; fruit a large head; trunks usually with basal proproots .... *Pandanus*
        6. Leaves not toothed; fruit a small berry; trunks without proproots .... *Cordyline*
    2. Herbs, vines, or creepers; including grasslike plants (these sometimes with tall, moderately rigid, canelike stems)
      7. Plants strictly aquatic, submerged or floating
        8. In salt water only; marine plants rooted in sand or sandy debris in quiet lagoon waters
          9. Leaves up to 3 ft long or more, mostly 12–17 mm wide; rooted portion with black persistent fibres
                .... *Enhalus*
          9. Leaves seldom as much as 1 ft long, 4–10 mm wide; rooted portion lacking black fibres .... *Thalassia*
        8. In fresh water only, floating or loosely rooting in mud .... *Blyxa octandra*
      7. Plants terrestrial, rooted in soil
        10. Grasses and grasslike plants (grasses, sedges, reeds), i.e., usually with sublinear leaves with parallel veins, but leaves sometimes reduced or absent; small green or brown flowers; tufts of fibrous roots
          11. Stems triangular in cross section; inflorescence surrounded by leaflike bracts
            12. Inflorescence a buttonlike head .... *Cyperus kyllingia*
            12. Inflorescence with evident branching
              13. Coarse plants to 5 ft tall .... *Cyperus odoratus*
              13. Slender herbs to 2–3 ft .... *Cyperus javanicus*
          11. Stems round or nearly so in cross section; inflorescence without or with rather inconspicuous bracts
            14. Stems solid; rosette plants
              15. Leafy plants with branched inflorescences
                16. Seeds brown .... *Fimbristylis*
                16. Seeds white .... *Scleria*
              15. Leafless plants with apical inflorescence on scapes .... *Eleocharis*
            14. Stems hollow, nodose; rosette or creeping plants
              17. Tall (to 9–12 ft) with canelike stems, large plumose inflorescences of minute slender spikelets
                18. Inflorescence green or brown; swamp reeds .... *Trichoon karka*
                18. Inflorescence white or silvery (sugarcane of gardens) .... *Saccharum officinarum*
              17. Not tall reeds
                19. Fruit a spiny burr .... *Cenchrus echinatus*
                19. Fruit not a spiny burr
                  20. Inflorescence narrow cylindric, breaking at joints when mature .... *Lepturus repens*
                  20. Inflorescence not jointed and disarticulating
                    21. Spikes digitate, 2 or more borne umbellately
                      22. Spikelets awned
                        23. Spikes 3–5; spikelets of several florets each, in several rows on lower side of rachis .... *Dactyloctenium*
                      23. Spikes usually 2; spikelets paired, 1 stalked, 1 sessile .... *Ischaemum*
                      22. Spikelets not awned
                        24. Spikelets each with 1 floret
                          25. Spikes 2, conjugate; fruit indurate, broader or broad as long .. *Paspalum*
                          25. Spikes usually 3 or more; fruit cartilaginous; longer than broad *Digitaria*
                      24. Spikelets each with several florets .... *Eleusine indica*
                    21. Spikes not digitate
                      26. Spikelets all on one side of rachis
                        27. Spikes several, distant; grass of shady forest .... *Oplismenus*
                        27. Spikes 1 or 2, close, hidden; beach grass .... *Thuarea*
                      26. Spikelets on both sides of rachis
                        28. Leaves elliptic, ½–1 inch wide; panicle large, pale, complex
                          .... *Centotheca lappacea*
                      28. Leaves narrow, less than ¼ inch wide
                        29. Spikelets minute, in a diffuse compound panicle; no awns .... *Eragrostis*
                        29. Spikelets in a stiff reddish few-branched panicle; awns present *Chrysopogon*
        10. Not grasses or grasslike plants; herbs, often very large or giant, as in bananas; or vines
          30. Leaves with reticulate (network) venation

31. Vines .... *Dioscorea*
31. Not vines
   32. Leaves palmately then pinnately divided; flowers on tall leafless scapes, in clusters bearing also long threadlike pendent filaments; tuberous .... *Tacca*
   32. Leaves not divided; leaves heart-shaped, with rounded or pointed (then arrow-shaped) lobes
      33. Large herbs with pointed (arrow-shaped) lobes .... *Cyrtosperma*
      33. Small or large herbs with rounded lobes
         34. Smaller plants, rarely over 3 or 4 ft tall, leaves pale or glaucous .... *Colocasia*
         34. Larger plants with dark leaves .... *Alocasia*
30. Leaves with parallel veins
   36. Terrestrial plants
      37. Giant herbs with oblong leaves 3–6 ft long, often 1 ft broad, later splitting into segments to the midrib; parallel veins perpendicular to midrib (bananas) .... *Musa*
      37. Smaller herbs with parallel longitudinal veins
         38. Tall herbs with leaves arranged alternately along the erect stems .... *Alpinia*
         38. Leaves basal from a short usually underground corm or bulb
            39. Leaves stiff and pointed, spiny; compound fruit with a crown of leaflike bracts .. *Ananas*
            39. Leaves otherwise; fruit not as above
               40. Large herbs (leaves to several ft long); flowers white
                  41. Flowers with a corona .... *Hymenocallis*
                  41. Flowers without corona .... *Crinum*
               40. Small herbs (leaves seldom to 1 ft long) with pink flowers ...... *Zephyranthes rosea*
   36. Epiphytes with short, somewhat leathery leaves; alternating on the stem ...... *Dendrobium* sp.
1. Dicotyledons (seed with 2 cotyledons; leaves usually with reticulate venation; taproot often present; woody species often with "solid," cambium-formed, annually incremented wood; flowers often in 4's or 5's or multiples thereof)
42. Leafless, often orange-stemmed parasitic vines .... *Cassytha*
42. Not as above
   43. Leaves compound, divided into fully distinct leaflets
      44. Leaves with 3 leaflets (in *Derris trifoliata* leaves of both 3 and 5 leaflets found)
         45. Trees or shrubs
            46. Leaflets with slightly toothed edges; fruit a round berry .... *Allophylus*
            46. Leaflets entire, smooth edged; fruit a short flat segmented pod .... *Desmodium*
         45. Vines or herbs
            47. Flowers yellow .... *Vigna marina*
            47. Flowers pink or white
               48. Flowers rosy pink, the banner petal with a white splotch; pod somewhat inflated; leaflets always 3, broadly ovate .... *Canavalia maritima*
               48. Flowers pale pink to white; pod very flat; leaflets sometimes 3, sometimes 5 .. *Derris trifoliata*
      44. Leaves with more than 3 leaflets
         49. Erect shrubs, or herbs
            50. Leaves 1-pinnate
               51. Flowers papilionate, 2 petals joined to form a keel, 2 petals as lateral wings, 1 as a banner; fruit an inflated pod .... *Crotalaria*
               51. Flowers mimosoid, not as above; fruit thick but not inflated .... *Cassia*
            50. Leaves bi- or tripinnate .... *Polyscias fruticosa*
         49. Vines or creepers
            52. Leaflets usually 5 or 7 per leaf, more than 1 inch long; plants seldom climbing .. *Derris elliptica*
            52. Leaflets more numerous but smaller; high climbers; seed small, red, with black spot *Abrus precatorius*
   43. Leaves simple or merely lobed or parted, not divided into distinct leaflets
      53. Leaves markedly lobed (not merely toothed)
          54. Trees, giant softwooded herbs, or herbs, with thick milky latex
            55. Herbs; upper leaves with basal red patches .... *Euphorbia heterophylla*
            55. Trees or tree-like herbs
               56. Leaves pinnately lobed (lobing quite variable, some trees with nearly entire leaves) *Artocarpus*
               56. Leaves palmately parted .... *Carica papaya*
          54. Vines or herbs; sap not milky
            57. Climbing vines
               58. Leaves mostly 3-lobed; flowers large, rotate, with an ornately laciniate calyx, not tubular .... *Passiflora foetida*
               58. Leaves 3- or mostly 5-parted; flowers tubular, trumpetlike; calyx not laciniate *Ipomoea digitata*
            57. Herbs or prostrate creepers (sometimes slightly woody)
               59. Prostrate creepers; fruit a burr .... *Triumfetta procumbens*
               59. Erect (somewhat woody) herbs
                   60. Fruit a burr; leaves mostly 3-lobed .... *Triumfetta semitriloba*
                   60. Fruit a hairy capsule; leaves mostly 5-lobed .... *Abelmoschus moschatus*
      53. Leaves not at all lobed, sometimes toothed
         61. Trees or large notably woody shrubs
            62. Sap milky white, or noticeably yellowish latex
               63. Sap yellowish; leaves with numerous curved parallel lateral veins; fruit a hard woody sphere of golfball size .... *Calophyllum inophyllum*

63. Sap milky; leaves not as above
  64. Old leaves turning red just before falling; fruit a small 3-celled capsule; latex poisonous .... *Excoecaria agallocha*
  64. Old leaves usually turning yellow; fruit a small "fig"; not poisonous
    65. Small, somewhat shrubby tree; leaves usually asymmetric at base; dioecious; figs orange .... *Ficus tinctoria*
    65. Large trees with aerial roots; leaves symmetric; figs pink .... *Ficus virens*
62. Sap clear, watery
  66. Mangrove trees with prominent aerial proproots or ascending breather-roots
    67. Leaves spirally arranged, longer than broad; stipules present
      68. Flowers with scarlet corolla, tubular; leaves narrowly obovate, often notched at tip; seed germinating after falling .... *Lumnitzera littorea*
      68. Flowers with inconspicuous white or orange petals (but calyx may be deep red); seed germinating on tree, radicle growing to a length of a foot or more before falling
        69. Calyx of 7–14 narrow lobes, usually red (rarely white); flowers shortly stalked, pendent .... *Bruguiera gymnorrhiza*
        69. Calyx of 4 short deltoid lobes, usually green
          70. Inflorescence branched, of several flowers .... *Rhizophora mucronata*
          70. Inflorescence short, of few flowers .... *Rhizophora apiculata*
    67. Leaves opposite, nearly as broad as long or broader; stipules absent .... *Sonneratia*
  66. Not mangrove trees as above
    71. Stamens fused into a tube surrounding the style; corolla tubular, yellow, of 5 petals; hibiscus-like flowers
      72. Leaves broadly cordate, grayish beneath, tip not much drawn out ...... *Hibiscus tiliaceus*
      72. Leaves narrowly cordate, green, tip long drawn out .... *Thespesia populnea*
    71. Stamens not fused as above
      73. Leaves pale beneath, covered closely by minute peltate scales; fruit a keeled, woody, boat-like structure .... *Heritiera litoralis*
      73. Leaves not as above
        74. Twigs thorny; foliage with odor of lime .... *Citrus*
        74. Not thorny; not with lime odor
          75. Leaves alternate or spiralled
            76. Leaves distichous (alternating in 1 plane)
              77. Flowers bisexual
                78. Leaves coarsely toothed; flowers yellow; a scrambling shrub
                  .... *Colubrina asiatica*
                78. Leaves entire; trees
                  79. Fruit muricate (with soft blunt thorns), edible ... *Annona muricata*
                  79. Fruit not muricate .... *Cananga odorata*
              77. Flowers unisexual .... *Glochidion*
            76. Leaves not distichously arranged
              80. Leaves peltate or nearly so
                81. Flowers bisexual; leaf entire with red spot at junction of petiole; fruit a black berry set inside a lantern-like calyx .... *Hernandia*
                81. Flowers unisexual; leaf with 3 large teeth and many small ones; without red spot; fruit a small capsule .... *Macaranga carolinensis*
              80. Leaves not at all peltate
                82. Leaves concave, saucerlike .... *Polyscias scutellaria*
                82. Leaves flat
                  83. Flowers unisexual; leaves coarsely toothed .... *Acalypha*
                  83. Flowers bisexual; leaves entire
                    84. Corolla orange .... *Cordia*
                    84. Corolla white, greenish, pink, or cream
                      85. Leaves mostly 1–2 inches long, crowded on stems, fleshy; flowers white with separate petals .... *Pemphis*
                      85. Leaves larger, mostly 4–16 inches long
                        86. Leaves elliptic, glabrous; fruit a mango .. *Mangifera indica*
                        86. Leaves obovate
                          87. Leaves pale, often softly hairy with indistinct veins; flowers in short cymes; berry white .... *Scaevola*
                          87. Leaves darker, with distinct veins; fruit not white
                            88. Flowers in narrow spikes, less than ¼ inch wide; fruit a red drupe .... *Terminalia*
                            88. Flowers in long racemes or clusters; fruit a green or brownish, angular, boxlike structure
                              89. Flowers pink, in long pendent racemes; fruit about 3 inches long, with rounded angles; tree of fresh-water swamps .... *Barringtonia racemosa*

89. Flowers white or faintly pinkish, in large not pen-
dent inflorescences; fruit 4–5 inches long, boxlike
with 4 (rarely 5) fairly sharp angles, seaside
tree .... *Barringtonia asiatica*
75. Leaves opposite
90. Stipules present; flowers white, regular
91. Fruit compound, fleshy, whitish, lumpy; flowers 4 or 5 petaled .. *Morinda*
91. Fruit not compound; flowers 8-petaled .... *Guettarda speciosa*
90. Stipules absent; flowers whitish or pale lavender, very small, 2-lipped .. *Premna*
61. Not trees; herbs (erect or prostrate) or vines
92. Leaves with petioles much longer than the cordate blades; low herbs with inconspicuous umbels of
small flowers .... *Centella asiatica*
92. Not as above
93. Sap milky
94. Small, more or less prostrate herbs
95. Hairy and purplish leaves .... *Euphorbia hirta*
95. Glabrous .... *Euphorbia thymifolia*
94. Erect, sometimes slightly woody herbs; all leaves pale green, entire .. *Euphorbia chamissonis*
93. Sap not milky
96. Leaves opposite
97. Stamens long, protruding from the corolla; woody climbing or scrambling vines
.... *Clerodendrom inerme*
97. Stamens included; small, somewhat woody, shrubby herbs
98. Flowers purple or blue, borne on spikes .... *Stachytarpheta*
98. Flowers white or yellow, not in spikes
99. Garden herbs with very pungent minty odor .... *Ocimum sanctum*
99. Wild or weedy plants without strong odor
99a. Leaves entire; flowers white .... *Hedyotis biflora*
99b. Leaves coarsely toothed, flowers yellow .... *Wedelia biflora*
96. Leaves alternate
100. Flowers yellow with clawed petals; erect herb of freshwater swamps ... *Ludwigia octovalvis*
100. Flowers greenish-white, minute, petals not clawed; herb of dry ground *Phyllanthus amarus*

TAXONOMIC CHECK LIST

PTEROPSIDA
Class FILICINAE (Ferns)

Acrostichum aureum L.

A giant fern of swamps, usually mingled with mangrove species; it may reach 10 or 12 ft in height. The fertile fronds are slightly smaller than the sterile, which may be 18 inches wide.

Asplenium nidus L. "nnuk"[2]

The birds'-nest fern. A large species, usually epiphytic, with long strap-shaped fronds forming a rosette; sporangia in oblique linear sori.

Cyclosorus goggilodus (Schkuhr) Link

A fern of swamps (fresh-water) and taro patches. Sometimes called *C. gongylodes*.

Davallia solida (Forst.) Sw.; "peceen attu" (5281)[3]

A common epiphyte with a long, scaly rhizome closely attached to trunks or branches, bearing broadly deltoid tripinnatifid fronds.

Nephrolepis exaltata (L.) Schott; "amääre" (5275)

Terrestrial, rarely epiphytic; fronds pinnate.

Phymatodes scolopendria (Burm.) Ching; "wënnümey" (5273)

Terrestrial or epiphytic; fronds deeply pinnately parted. Also called *Microsorum* ("*Microsorium*") *scolopendria*.

Class ANGIOSPERMAE (Flowering Plants)
Subclass MONOCOTYLEDONAE
PANDANACEAE

Pandanus carolinensis Martelli; "fach"

HYDROCHARITACEAE

Blyxa octandra (Roxb.) Planch. ex Thw.

The flowers of this aquatic plant are borne at the end of narrow scapes and are minute.

[2] The vernacular names given are in the orthography used by Prof. Goodenough, and fuller rules on pronunciation will be found in his works. It should be noted here, however, that *c* is equivalent to *j* as in *just;* and that doubled vowels indicate extension of the sound.
[3] These numbers refer to the author's collections,

the originals of which are deposited in the College of Guam Herbarium; duplicates have been sent to the Bishop Museum, Honolulu, and to the U. S. National Herbarium.

Enhalus acoroides (L.f.) Rich. ex Chatin
In lagoons; more common than *Thalassia*.

Thalassia hemprichii (Ehrb.) Aschers.

GRAMINEAE

PANICOIDEAE group
Tribe ANDROPOGONEAE

Ischaemum muticum L; "fetinin wuumw" (5285)
Chrysopogon aciculatus (Retz.) Trin.
Saccharum officinarum L; sugarcane

Tribe PANICEAE

Cenchrus echinatus L; burgrass
Digitaria pruriens (Fisch. ex Trin.) Buse var. *microbachne* (Presl) Fosb.
Oplismenus compositus (L.) Beauvois
Paspalum orbiculare Forst.
Thuarea involuta (Forst. f.) Roemer and Schultes

POOIDEAE group
Tribe FESTUCEAE

Centotheca lappacea Desvaux.; "fetinin wum-wunë" (5284)

Tribe ARUNDINEAE

Trichoon karka (Retz.) Roth in Roem. (5289)
Hitherto generally known as *Phragmites karka* (Retz.) Trin. ex Steudel. Unfortunately this name cannot be maintained; see Stone (1964).

Tribe ERAGROSTEAE

Eragrostis amabilis (L.) Wight and Arnott
Dactyloctenium aegyptium (L.) Willd.
Eleusine indica (L.) Gaertner

Tribe LEPTUREAE

Lepturus repens (Forst.) R. Brown

CYPERACEAE

Cyperus javanicus Houtt.
Cyperus kyllingia Endl.

Cyperus odoratus L. (5305)
Cyperus sp.
Eleocharis geniculata (L.) Roemer and Schultes (5300)
Fimbristylis cymosa R. Br. (5314)
Scleria sp. (5306)

PALMAE

Cocos nucifera L.; coconut palm

Metroxylon amicarum (Wendland) Beccari; ivory-nut palm
Generally in standing water or wet locations in valleys.

Nypa fruticans Wurmb.
The nipa palm. Easily recognised by its trunkless appearance in swamps.

ARACEAE

Alocasia macrorrhiza (L.) Schott ex Schott and Endlicher
Colocasia esculenta (L.) Schott; taro
Cyrtosperma chamissonis (Schott) Merrill

BROMELIACEAE

Ananas comosus (L.) Merrill; pineapple
Occasionally in cultivation.

AGAVACEAE

Cordyline fruticosa (L.) Goepp.
Hitherto known as *Cordyline terminalis* (L.) Kunth (see Stone, 1964).

AMARYLLIDACEAE

Crinum asiaticum L.; spider-lily
Hymenocallis littoralis (Jacq.) Salisb.; seaside-lily
Zephyranthes rosea (Sprengel) Lindley

TACCACEAE

Tacca leontopetaloides (L.) O. Kuntze (5309)

DIOSCOREACEAE

Dioscorea bulbifera L.?; yam (5366)

MUSACEAE

Musa balbisiana X *acuminata* (*M. paradisiaca* L.); banana

ZINGIBERACEAE

Alpinia purpurata (Vieill.) K. Schumann; red ginger

ORCHIDACEAE

Dendrobium sp.; nikocopwcopw" (5282) Epiphytic. A native species.

Subclass DICOTYLEDONAE

PIPERACEAE

Peperomia pellucida (L.) HBK.
Piper sp., "enes" (5274)

MORACEAE

Artocarpus altilis (Park.) Fosb.; breadfruit
Ficus tinctoria Forst. f. (5298, 5310)
Ficus virens Ait.; "aaw" (5291)
Hitherto known as *F. carolinensis* Warb. (see Corner, 1965).

URTICACEAE

Procris pedunculata (Forst. f.) Wedd.; "kimm-wit" (5292)

POLYGONACEAE

Polygonum minus var. *procerum* (Danser) Steward? (5303)
[If this is the same as the *Polygonum* in Guam.]

ANNONACEAE

Annona muricata L.; soursop
Cananga odorata (Lam.) Hook. f. and Thomson; ylangylang

LAURACEAE

Cassytha filiformis L.

HERNANDIACEAE

Hernandia sonora L.

LEGUMINOSAE

Abrus precatorius L.; prayerbead
Cassia occidentalis L.; coffee senna
Canavalia maritima (Aublet) Thouars; seaside peavine, "cëëcon" (5272)
Crotalaria sp.; "afanafan" (5283)
Derris elliptica (Roxb.) Bentham; "wüüp" (5276)
Derris trifoliata Loureiro; "wunenipot" or "wupenipot"
Desmodium umbellatum (L.) DC.
Vigna marina (Burm.) Merr.

RUTACEAE

Citrus aurantifolia (Christm.) Swingle; lime, "näyimis" (5277)

EUPHORBIACEAE

Acalypha trukensis Pax and Hoffman; "mön-now" (5270)
An endemic small tree, fairly common throughout Truk.

Euphorbia chamissonis (Klotszch and Garcke) Boissier (5313)
Euphorbia heterophylla L.
Euphorbia hirta L.
Excoecaria agallocha L. (5294)
The sap of this tree is reputedly dangerous, especially to the eyes. It may be recognized by its prevalence in or near mangrove swamps or rocky seaside locales, the tendency for the mature leaves to turn red before falling, and the small catkins of flowers. The sap is notably milky.

Glochidion ramiflorum Forst.?; "afor" or "ofor" (5365)

Macaranga carolinensis Volkens; "tuupw" or "kuruwen" (5271)
Endemic in the Caroline Islands.

Phyllanthus amarus Schum. and Thonn.

ANACARDIACEAE

Mangifera indica L.; mango

SAPINDACEAE

Allophylus timorensis (Bl.) DC. (5311)

RHAMNACEAE

Colubrina asiatica (L.) Brongniart

TILIACEAE

Triumfetta procumbens Forst. f. (5308)
Triumfetta semitriloba Jacq.?; "sacawer" (5280)

MALVACEAE

Abelmoschus moschatus (L.) Medik; "nikönö- köön" (5288)
Hibiscus tiliaceus L. (5290)
Malvastrum coromandelianum (L.) Garcke; "siyöyinen" (5286)
Thespesia populnea (L.) Solander ex Correa

STERCULIACEAE

Heritiera littoralis Dry. (5299)
Copiously fruiting, Jan. 28, 1965.

GUTTIFERAE

Calophyllum inophyllum L.; *kamani* or Alexandrian laurel

CARICACEAE

Carica papaya L.
Only a few seen.

PASSIFLORACEAE

Passiflora foetida L. var. *hispida* (DC.) Killip; "pwompwom" (5279)

LYTHRACEAE

Pemphis acidula Forst.
Apparently rare on Romonum; only one individual seen.

RHIZOPHORACEAE

Bruguiera gymnorrhiza (L.) Lam.
Also called *B. conjugata* (L.) Merrill. The usual form has the calyx scarlet; a form with a pure white calyx was described from Namonuito (Stone, 1959). This requires a nomenclatural adjustment, as follows:

Bruguiera gymnorrhiza forma *alba* B.C. Stone, comb. nov.
B. conjugata (L.) Merr. forma *alba* B.C. Stone, Pacific Sci. 13:102 (1959). Type: Namonuito, Pisarach Islet, 2 July 1957, *Stone* 2144 (BISHOP MUSEUM). N.v. "ong."

Rhizophora apiculata Bl.; "ciyaan iimw"
Rhizophora mucronata Lam.; "ciyaan wuumw" (5297)
Since *Rhizophora stylosa* Griff. has been reported from Guam (*Stone* 4437, GUAM and LEIDEN) by Ding Hou (in litt.), it may turn up in other parts of Micronesia also. The three species are distinguished in Flora Malesiana (Ser. I, vol. 5, part 4, p. 450), 1958, as follows:

1. Inflorescences 2-flowered, shorter than the petiole, in the axils of leaf scars of last year's or last season's growth; bracteoles at the base of the flower completely connate; petals glabrous . . . . *R. apiculata*
1. Inflorescences 2–16-flowered, longer than the petiole, in the axils of current year's or season's growth; bracteoles connate only at base; petals hairy
2. Style obscure or very short, to 1.5 mm long . . . . *R. mucronata*
2. Style filiform, 4–6 mm long . . . *R. stylosa*

Since only the first two species are recorded in Kanehira's check list of the Micronesian flora (1935), it will be of interest to see if the occurrence of *R. stylosa* elsewhere in Micronesia can be established.

SONNERATIACEAE

Sonneratia caseolaris (L.) Engler (5295)

COMBRETACEAE

Lumnitzera littorea (Jack) Voigt (5293)
Terminalia samoensis Rechinger

LECYTHIDACEAE

Barringtonia asiatica (L.) S. Kurz
Barringtonia racemosa (L.) Blume (5302)

ONAGRACEAE

Ludwigia octovalvis (Jacq.) Raven, Kew Bull. 15:476 (1962). (5304)
Hitherto known as *Jussiaea suffruticosa* L.

ARALIACEAE

Polyscias fruticosa (L.) Harms.
Polyscias scutellaria (Burm. f.) Fosb.
Polyscias pinnata Forst. cultivar "tricochleata"

UMBELLIFERAE

Centella asiatica (L.) Urban

CONVOLVULACEAE

Ipomoea digitata L. (5367)
Ipomoea indica (Burm. f.) Merrill
The same as *I. congesta* R. Br.

BORAGINACEAE

Cordia subcordata Lam. (5312)

VERBENACEAE

Clerodendron inerme (L.) Gaertner
Premma obtusifolia R. Br. (5307)
Stachytarpheta jamaicensis (L.) Vahl; "sakura" (5287)
The vernacular name, obviously Japanese (sakura = cherry), indicates the relative recency of this plant's introduction. Informants placed the first appearance of the species in the 1920's.

LABIATAE

Ocimum sanctum L.; "warüg" (5278)
Cultivated as an herb used with fish. The herbage is very rank.

ACANTHACEAE

Blechum ?brownei

RUBIACEAE

Guettarda speciosa L.
Hedyotis biflora (L.) Lam. (5367-a)
Morinda citrifolia L.

GOODENIACEAE

Scaevola taccada (Gaertn.) Roxb.
Variously called *S. frutescens* or *S. koenigii* in older literature. Also known as *S. sericea* Vahl.

COMPOSITAE

Wedelia biflora (L.) DC. (5296)
Vernonia cinerea (L.) Less.

ECOLOGICAL NOTES ON THE VEGETATION OF ROMONUM

Major Patterns of Vegetation

Very little, if any, of the original vegetation is left intact. Instead the island presents a picture of the long-existing interaction of man on the insular environment. Because of the small size and low elevation of the island, every square foot has probably had, from time to time at least, the imprint of the human foot or the effects of the agricultural hand. In fact, throughout Truk, it is difficult to envision what the original lowland vegetation was like except in the areas which, because of their marginal nature—such as mangrove swamps, freshwater swamps, and sandy beach areas—have been considered useless or too difficult to change. Of course, in the more advanced areas (e.g., Moen) even these areas are now much altered through the use of modern techniques and machinery. On Romonum, however, we may look to these marginal areas for at least a partially persistent element of pre-human vegetation.

Outside these marginal areas, Romonum consists largely of cultivated trees, usually rather well spaced, and consisting primarily of coconut palms and breadfruit trees. These two species are the only large trees in some localities, especially in the immediate neighborhood of houses. On the hill in the eastern part, and toward the central part of the island, mango trees are also found in considerable numbers. Wherever "villages" are located quite near the coast, there are small numbers—sometimes single individuals—of various arborescent species, especially *Hernandia sonora*, *Ficus virens*, *Metroxylon amicarum*, *Calophyllum inophyllum*, *Hibiscus tiliaceus*, or *Thespesia populnea*. Although there are exceptions, the mangrove trees—

FIG. 3. View of the south coast of Romonum looking slightly eastward. (The pier of basalt rocks is that shown on the map just short of the western tip of the island.) The appearance is very characteristic, with the numerous coconut palms. The tree at the left is a *Hernandia*.

Rhizophora, Bruguiera, Lumnitzera, Sonneratia, Excoecaria—and the littoral *Heritiera* are seldom found very near houses. To summarize, then, the major visual aspect of the forested portions of the island is the predominance of *Cocos, Artocarpus,* and scattered individuals of *Mangifera, Ficus,* and occasional other trees.

Other than this fairly homogeneous and largely man-made "forest" type, several other major features are evident. These are the mangrove forest; the freshwater swamps; the sandy beach; and the basalt-boulder coast.

Mangrove Formation

Tree species: *Rhizophora mucronata, R. apiculata, Bruguiera gymnorrhiza, Sonneratia caseolaris, Excoecaria agallocha, Nypa fruticans, Lumnitzera littorea.*

Other characteristic species: *Acrostichum aureum.*

Marginal species: *Hibiscus tiliaceus;* species of the freshwater swamps, which to some extent interpenetrate the mangrove area.

In general, the Micronesian mangrove formations are not as rich in species, or so productive in individuals, or so notable for large trees, as are the formations in the Malaysian or Caribbean areas. In turn, the mangrove areas in Truk are rather less rich in species than those of Palau, farther west and consequently nearer the vast Philippine mangrove regions. Such species as *Scyphiphora hydrophyllacea* (Rubiaceae), *Dolichandrone spathacea* (Bignoniaceae; occasional at margins of mangrove areas), and *Ceriops candolleana* (Rhizophoraceae), although found in Palau (and Yap) do not occur in Truk,

FIG. 4. The swamp fern, *Acrostichum aureum,* in the foreground; behind, a marginal zone of *Trichoon karka,* with intermixed coconut palms.

Ponape, Kusaie, the Marianas, or the Marshall Islands. Many other mangrove formation plants, common enough in Malaysia and the Philippines, do not occur anywhere in Micronesia (e.g., *Aegiceras, Kandelia,* other species of *Rhizophora*). *Xylocarpus granatum* occurs elsewhere in Truk, but I did not find it in Romonum.

Rhizophora stylosa Griff. has been found in Ponape (*Stone* 1773) and in Guam (*Stone* 4437) and probably occurs in Truk also.

The mangrove formation of Romonum is on the whole rather poorly developed. The one extensive area is on the southern side of the island, from about the middle to within a few hundred yards of the east end. Small parts of the periphery have been converted to taro (*Colocasia*) or *Cyrtosperma* plots. The larger central area of the swamp is composed of scattered and

fairly small individuals of the various species, seldom over 10 ft high, interspersed with clumps of *Acrostichum.*

Freshwater Swamps

All of these are now to some extent planted with taro or *Cyrtosperma,* but they also include, to quite varied extent, various other species. Some swamps have been essentially cleared of vegetation, which has then been replaced by the cultivated aroids. Others, perhaps abandoned at various times of earlier cultivation, have become overrun with "weedy" species or with invading native elements. In time the freshwater swamp trees, *Barringtonia racemosa* and *Metroxylon amicarum,* become a conspicuous feature (Fig. 6). Also, the periphery of such swamps is constantly undergoing slight changes, depending on the adjacent area; advancing on

FIG. 5. Ivory-nut palms (*Metroxylon amicarum*) in the west freshwater swamp. Below, left and right, clumps of *Cyrtosperma chamissonis*. Center, *Trichoon karka*.

or retreating from them in accordance with such factors as rainfall, changes in tides, or man's activities.

Tree species: *Barringtonia racemosa, Metroxylon amicarum*. Some other trees are also to be found in or at the edges of these swamps; they exhibit varying degrees of tolerance to standing water. Some, for example *Glochidion*, may endure the swamp conditions for an appreciable time, but succumb eventually, and meanwhile present an unhealthy appearance, the leaves being few and often chlorotic. Typically, only the *Barringtonia* and *Metroxylon* are bona fide members of such swamp communities, and even the *Metroxylon* is not restricted to such communities but, for example, as on Tol Island, may be found in moist rocky valleys.

Other characteristic species: the aroids, either actively cultivated or persisting from former cultivation (*Colocasia, Cyrtosperma*, and, rarely, *Alocasia*); the tall reed *Trichoon karka; Ludwigia octovalvis; Polygonum minus; Cyperus odoratus;* other Cyperaceae on occasion (*Cyperus* sp., *Eleocharis geniculata, Scleria*); the fern *Cyclosorus goggilodus;* the aquatic *Blyxa octandra.*

Marginal species: *Hibiscus tiliaceus, Acrostichum aureum.*

Sandy Beach Formation

(*Cocos* and *Artocarpus* must be included also.)

Tree species: (1) Canopy trees—*Hernandia sonora, Calophyllum inophyllum* (scarce on Romonum), *Barringtonia asiatica, Thespesia populnea, Pandanus* (rarely). (2) Understory or smaller trees, or large shrubs—*Scaevola taccada, Guettarda speciosa, Premna integrifolia,*

FIG. 6. The ivory-nut palm, *Metroxylon amicarum*.

Morinda citrifolia, Allophylus timorensis, Ficus tinctoria, Terminalia samoensis, Cordia subcordata.

Climbing vines or scrambling low shrubs: *Clerodendron inerme, Piper* sp., *Wedelia biflora, Colubrina asiatica, Cassytha filiformis.*

Prostrate vines: *Canavalia maritima, Vigna marina.*

Herbs or shrubs of low stature (generally less than 1 ft high): *Euphorbia chamissonis, Triumfetta procumbens,* the grasses *Lepturus repens, Thuarea involuta,* and the sedge *Fimbristylis cymosus.*

Erect herbs: *Tacca leontopetaloides, Crinum asiaticum, Nephrolepis.*

Epiphytes: *Phymatodes scolopendria* (also terrestrial on occasion), *Davallia solida, Dendrobium* sp., *Asplenium nidus.*

These weedy grasses frequently are found in sand: *Eragrostis amabilis, Cenchrus echinatus, Dactyloctenium aegyptium,* and, less commonly, *Eleusine indica. Euphorbia hirta* and *E. thymifolia, Passiflora foetida,* and *Stachytarpheta jamaicensis* are all found around houses near the beach.

Except for the absence of certain species (e.g.,

Messerschmidia argentea, Soulamea amara, Suriana maritima, etc.) the plants enumerated here would be found on the reef islets of Truk and on most atolls in Micronesia as well.

Rocky Coastal Vegetation

Trees: *Ficus virens, Heritiera littoralis, Barringtonia asiatica, Thespesia populnea, Hibiscus tiliaceus.*

Shrubs: *Allophylus timorensis, Desmodium umbellatum, Pemphis acidula.*

Herbs, low shrubs, or vines: *Derris trifoliata* (generally prostrate, but also a climbing vine), *Nephrolepis, Procris pedunculata, Wedelia biflora.*

Areas Under Cultivation, Past or Present

This term is preferable to a specific one indicating a formation, since so little evidence of a recognizable indigenous formation is left. As such it is a loose heading under which may be assembled the various "villages" (really small groups of houses) with their immediate environs, as well as the entire inner or central portion of the island (including the hill area) in which only a few scattered houses occur, but throughout which there are nearly continuous signs of either present or former cultivation. This is often not intensive nor extensive, but may consist of one or a few fruit trees (limes, soursops, *Carica papaya,* the edible pandans, mango) scattered under virtually continuous cover of coconuts, breadfruits, and occasional mangoes or large *Ficus,* and mixed with such relatively persistent, aggressive, or fast-growing noncultivated species as *Acalypha indica, Macaranga carolinensis,* and *Glochidion ?ramiflorum;* with ornamental species such as *Cananga odorata* or *Cordyline fruticosa;* or with occasional native species which may be remnants of an earlier type of vegetation or perhaps are randomly opportunistic individuals of other formations, usually at the margins of their area (e.g., *Premna, Pandanus, Hernandia*).

The ground-cover species (in the sense of being at ground level—these may be scatttered rather than continuous) include a number of weeds, such as *Euphorbia heterophylla, Malvastrum, Triumfetta semitriloba,* and the weedy grasses. Most evident is the very extensive cover

FIG. 7. *Phymatodes scolopendria* growing epiphytically on a branch of *Hernandia sonora* on the west beach of Romonum.

formed, usually jointly, by *Ischaemum muticum* and *Derris elliptica*. In small clearings may be found *Cassia occidentalis, Ipomoea digitata, I. indica, Dioscorea,* and *Abrus precatorius.*

In gardens around houses, or on old house sites, and also sometimes at random in various parts of the higher parts of the island, will be found ornamental species and hedgerow species, i.e., *Polyscias* (various species), *Zephyranthes rosea, Hymenocallis,* bananas, variegated leaf pandans, *Ocimum sanctum* (used as a flavoring), *Cordyline fruticosa,* the aroids, and *Cananga.*

In the west-central part of the island are the remains of the former Japanese colonial administration unit, with school, baths, well, generator plant, and other structures now mostly reduced to mere foundations or walls. In this

area there are several ornamentals not found elsewhere.

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A Hitherto Unrecorded Midge Gall of *Myrsine australis* (A. Rich.) Allan

B. C. Arnold[1]

Stem galls on *Myrsine australis* were reported by Lamb (1960) in his checklist of New Zealand Zoocecidea, but there appears to be no record yet of the conspicuous bud galls (Fig. 1) found near the branch extremities of this handsome tree, which is readily recognized by its red, mottled leaves, red stems, and dark red bark (Allan, 1961). When cut open, the dark bud galls may be seen to contain small white midge larvae or pupae in various stages of metamorphosis.

The present report is concerned chiefly with anatomical modifications of the leaf bud by the midge larvae.

METHODS AND MATERIALS

Galls of *Myrsine australis* were examined on trees in the forest over a period of 16 months, and specimens for histological examination were fixed in Formo-acetic-alcohol. Serial sections were cut at 10μ and stained in Safranin and Fast Green (Johansen, 1940). Freehand sections of living galls were made to observe the details of nutritive tissue which is slightly distorted by the fixative.

Pupae were removed from galls and left in small stoppered glass vials to transform into adult midges.

Artificial formation of the galls was attempted by removing small larvae from galls and placing them on tender buds of stem cuttings. The cuttings were kept under bell jars in the south light of the laboratory window, with the base of the cuttings immersed in tap water in small flasks.

OBSERVATIONS

New galls were first apparent in December as dull olive-green, budlike structures (Fig. 1).
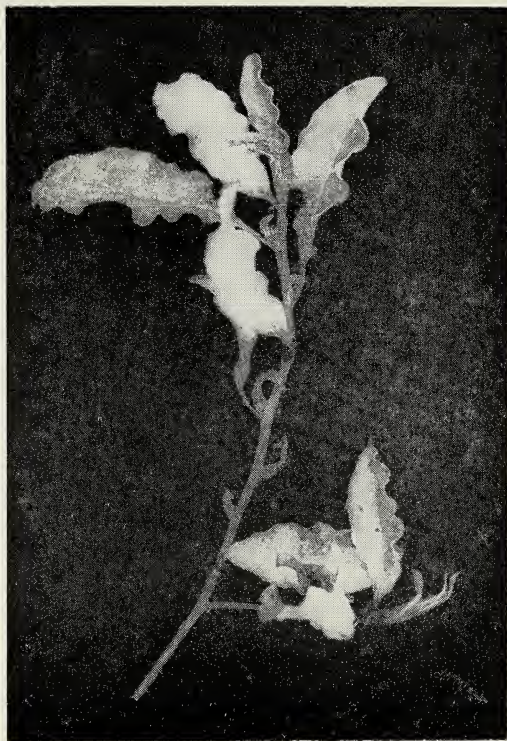
FIG. 1. Bud galls of *Myrsine australis*.

Within two months they had become almost black outwardly, masking the chlorophyll and red pigmentation of the internal tissues. During a mild spell of weather in winter, a few additional young galls were formed in June, but this would seem to be an exceptional event.

Under natural conditions in the forest, galls appear to live 10–12 months. By the following spring most galls are shrivelled and dry.

Mature galls range from $\frac{1}{4}$ to $\frac{3}{4}$ inch in length. Frequently the terminal gall of a branchlet may dominate the subjacent lateral galls (Fig. 2).

The midge larvae are small and white with prominent salivary glands containing polytene banded chromosomes. The larvae transform within the gall into small black pupae with prominent eyes which are crimson at first and

FIG. 2.   Large terminal gall and three smaller galls.

later dark purple. The adult fly is shining black with simple, fragile wings.

In the laboratory some flies emerged in autumn, probably in response to the high indoor temperatures.

When young larvae were removed from galls and placed on the soft tips of new shoots in the laboratory, they made no attempt to enter the new host plant. (In other experiments by the author with the gall moth *Morova subfasciata* Walk., the larval insect was capable of re-entering new shoots of the host after removal from the galls.) The attempt to elicit new galls on *Myrsine australis* with living larvae of the midge was unsuccessful, therefore.

It is readily apparent that each gall is composed of two or three modified leaves which are fused together.

A trace of the leaf blades may be seen at the top of the gall. Evidently the gall is derived chiefly from swollen petioles, which are curved and fused together to form a small urnlike structure occupied by one or more larvae.

There is some variation in the degree of fusion of the modified leaves which form the

walls of the gall. Where the leaf margins are merely closely pressed together, a boundary is recognizable; in other cases the cells of each contributing swollen leaf are completely interknit, leaving no demarcation.

Some galls are partitioned into two compartments, and others contain only a single loculus. The number of larvae per gall ranges from one to four, the larger galls generally containing more larvae than the smaller ones.

In living galls the vaselike cavity is lined by nutritive tissue which may bear finger-like cells
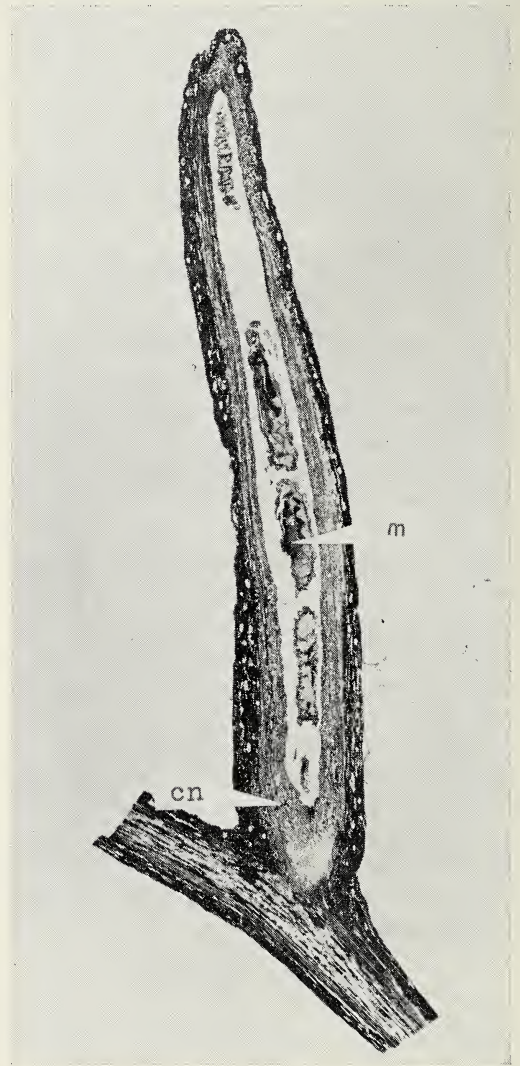
FIG. 3.   Longitudinal section through a large gall. *cn*, Chlorophyllous nutritive parenchyma; *m*, midge larva.

FIG. 4. Detail of Figure 3. *v*, Vascular strand; *cn*, chlorophyllous nutritive tissue; *c*, larval cavity; *e*, epidermis of gall.

projecting inwards. The concave base of the cavity is composed of chlorophyllous nutritive parenchyma (Fig. 3) which continues to multiply as the larvae feed. This growth ceases soon after the larvae discontinue feeding.

No remnant is left of the shoot apical meristem which originally gave rise to the two or three primordial leaves. In the development of galls at stem tips, increase in length of the branch is therefore curtailed at the same time as the leaf primordia are converted, under the influence of the larvae, into a gall.

The internal anatomy of the gall is rather more stemlike than leaflike, lacking as it does the characteristic stomatal arrangement and associated organisation of palisade layers and spongy mesophyll.

A very prominent cuticle extends over the gall epidermis and is continuous with the equally thick cuticle of the normal epidermis of the supporting stem.

Apart from the nutritive tissue surrounding the larvae, the histological features of the galls are the same as are found in the normal stem, namely: red pigmented cells, secretory cells, schizogenous cavities and canals with yellow or reddish brown contents, and normal vascular tissue (Metcalfe and Chalk, 1950).

DISCUSSION

A study of the life cycle of the gall midge was not undertaken, and the record of emergence of adult flies in autumn in the laboratory appears to be unseasonal, and related to higher average temperatures than those prevailing out of doors.

It would seem that the main morphogenetic changes accompanying gall formation are a suppression of the activity of the marginal meristems of the leaf primordia togteher with the eventual destruction of the shoot apical meristem from which the leaf primordia arose. There is evidence of limited growth of the leaf apex.

The bulk of the tissue appears to be con-

tributed by the swollen and fused petioles. These leaf parts are the nearest to the larva which occupies the former site of the shoot growing point.

Substances emanating from the larva might tend to stimulate growth in basal parts of a rudimentary leaf and these regions might undergo cell division and growth at the expense of other parts of the unformed leaves. Fusion of the basal parts of rapidly multiplying leaf primordia could readily occur, assisted possibly by wound hormones and larval secretions. These would be free to operate without the overriding influence of the shoot apical meristem.

In paraffin sections stained in Safranin and Fast Green, the salivary glands of larvae show characteristic giant cells with banded polytene chromosomes.

The synthetic activities of the salivary gland cells not only may assist feeding of the larvae but also may provide the secretions which are responsible for the transformation of presumptive leaf primordia to galls (Mani, 1964).

SUMMARY

A bud gall of *Myrsine australis* (A. Rich.) Allan caused by a gall midge is reported for the first time.

The galls are composed of modified leaves which form the walls of an urnlike structure enclosing the midge larvae or pupae.

The larvae feed on proliferating chlorophyllous tissue which lines the larval cavity.

During the development of the gall from a shoot bud, the apical meristem is destroyed by the larvae, and the leaf rudiments undergo transformation and fusion.

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An Unusual Example of Pseudoseisms[1] Resulting from Military Exercises[2]

Harold L. Krivoy, Charles G. Johnson, and Robert Y. Koyanagi[3]

ABSTRACT: Aerial bombing of the target island of Kahoolawe, Hawaii, during several hours on 19 and 20 December 1961 and on 13 February 1962 generated acoustic disturbances that were felt by people and recorded by seismometers on the island of Hawaii. The azimuth of arrival of the pseudoseisms was calculated from the accurate seismographic responses. Special atmospheric conditions are suspected as prime agencies in the propagation and focusing of these phenomena; lack of specific data in this field, however, leaves the matter of atmospheric structure speculative.

MANY COMMUNITIES have been disturbed by sonic booms created by high-speed aircraft. This problem has not yet become serious on the island of Hawaii, which has only recently established jet facilities. Nonetheless, series of disturbances resembling sonic booms were felt and recorded on Hawaii during several hours of the evening of 19 December 1961, the morning of 20 December 1961, and the evening of 13 February 1962. Since the affected neighborhoods are in a zone of active volcanism, prompt differentiation between artificial and natural events is a problem of immediate concern to the population and to the authorities.

From the results presented here, it seems possible that careful study of the character and timing of sonic disturbances recorded on Hawaiian seismographs by experienced seismologists may permit prompt identification of the source. Other experiments under more controlled conditions have already revealed important facts about energy distribution, refraction paths, etc. between the source and the receptors.

EVENTS LEADING TO THIS STUDY

Between 19:00 and 20:00 (HST) on 19 December 1961, an unusual variety of sensa-

tions were both felt and recorded on the island of Hawaii. Personnel of the U. S. Geological Survey's Hawaiian Volcano Observatory at Hawaii Volcanoes National Park, who were at their homes about 3 miles from the observatory, were aware of explosive shocks. When they reached the observatory they inspected the recordings being written by the high-gain, short-period, vertical seismographs at Desert, Uwekahuna, Ahua, and Mauna Loa stations. They recognized that the "pattern" of data as written by the Desert seismograph had been repeated by the Ahua seismograph after a lapse of about 17 seconds. (See Fig. 1 for station locations.) The observatory personnel assumed that these were sonic disturbances, and that they were not seismic events which would have swept the 15-km net in less than 2 seconds. At about the time the shocks were felt in the National Park area they were also felt by residents in the communities of Volcano, Hilo, and Kaumana. Civil Defense officials, alerted by many reports, called the observatory and were advised of the results of the seismogram analysis.

During the evening, all possible local noise sources were checked carefully. Explosive volcanism, though rare at Hawaiian volcanoes, is always a possibility. In this case, the lack of reports from Kona seemed to rule out eruption of the dormant volcano Hualalai. A radio check with personnel at the U. S. Weather Bureau, Mauna Loa Slope Observatory, 6 miles from the summit caldera of Mauna Loa, indicated that no one there had felt, heard, or sensed the dis-

FIG. 1.   Locations and elevations, in meters, of U. S. Geological Survey seismometers (*circles*) on Kilauea and a constructed sonic wave front based on data picked up by the seismometers.

turbances, thus eliminating Mauna Loa as a source. Gunfire from the U. S. Army base at Pohakuloa, which is often heard by Hilo and Volcano residents during training exercises, was ruled out as a possible cause when it was learned that the base was then inactive.

INTERPRETATION OF RECORDED DATA

All four seismometers are timed from the same master clock, and accurate comparison of events recorded by these instruments is possible. Figure 2, a copy of the Desert seismogram, shows the disturbances described above, as well as those of a few local earthquakes for comparison. As the Desert seismometer seemed to be most sensitive to the sonic arrivals, its record was used in compiling a master list, which includes every suspicious event recorded during

the disturbed period. The Uwekahuna seismograph has a response similar to that of the Desert, although it is recorded optically. All events on the Uwekahuna record are shown in Table 1. Records from the Mauna Loa and Ahua instruments are similar to those from Desert. As stated above, events recorded on Desert were recorded on Ahua 17 seconds later.

The next morning, 20 December 1961, observatory personnel noticed renewed activity on the Desert record. People in the Hilo area, who perhaps were alerted by the events of the previous evening, called the observatory, and, as was the case the evening before, reported that they had experienced an audible sensation rather than a physical one, and that windows vibrated strongly and wall clocks shook. With the expectation that Mauna Loa should be the first local station to record these events, the gain on that

TABLE 1

ARRIVAL TIMES AT SUMMIT STATIONS OF SONIC DISTURBANCES
FROM THE EVENTS OF 19 DECEMBER 1961
(Numbers in parentheses are recorded double-amplitudes, in millimeters)

DESERT	UWEKAHUNA	AHUA	MAUNA LOA
18-29-06.3(3)			
29-35.3(3)			
31-37.2(6)			
31-42.8(14)			
35-42.8(4)			
39-54.3(12)	54.6(5/2)	40-11.6(5)	18.1(5)
40-36.9(7)			
40-39.8(10)			
40-58.3(34)	59.1(4)	41-16.0(14)	22.1(5/2)
43-16.8(23)	17.5(3)	34.5(21)	
43-46.7(38)	47.5(2)	44-04.6(16)	
44-24.8(19)	26.3(1)	42.5(4)	
44-56.3(21)	57.0(2)	45-14.1(6)	
47-32.8(8)	33.5(5/2)		
47-56.9(7)	57.8(4)	48-14.5(2)	
48-28.8(47)	30.0(8)	45.6(7)	47-53.2(2)
48-49.5(21)	50.1(2)	49-06.9(2)	
51-41.5(5)	42.0(5/2)	58.7(5)	
52-07.5(14)	08.0(3)	24.9(6)	51-31.5(1)
52-40.6(10)	41.4(2)		04.9(3/2)
55-48.1(11)	48.6(5/2)	56-05.4(3)	12.0(5)
56-21.0(4)	21.5(4)	38.3(4)	55-45.0(5/2)
56-46.3(5)	46.7(4)	57-03.6(5/2)	10.1(3/2)
59-09.2(2)			
59-48.5(5)	49.4(7/2)	00-07.5(3)	
19-26-42.1(10)	40.6(4)	57.6(8)	
27-14.1(18)	16.3(2)	31.5(5/2)	
27-49.5(27)	49.5(5)	28-06.4(8)	
30-57.0(2)			
31-40.3(5)	40.6(4)	55.6(1)	
32-37.4(12)	37.7(6)	53.0(3/2)	04.0(2)
35-14.0(5)	16.3(3/2)	33.7(2)	
36-08.1(5)	07.2(2)	25.7(3)	35-31.8(2)
36-58.5(3)			
38-56.1(10)	56.4(4)	39-13.4(5)	
39-51.0(22)	50.5(5)	40-08.5(11)	39-15.2(3/4)
41-01.1(19)	01.2(6)	18.6(5)	
48-53.8(3/2)			
20-34-35.8(2)	48.6(1)		

amplifier was increased greatly. The gain on the Ahua amplifier was also increased. The data listed in Table 2 generally bear out the observations suggested by Table 1. In Figure 3 are shown other locations at which there are instruments similar to that at Uwekahuna. It is interesting that such instruments on Maui and at Kamuela, Naalehu, Hilo, and Pahoa on Hawaii all failed to record these events. Furthermore, residents and police at these places, as well as along the west and northeast coasts of

Hawaii, who were questioned later, reported no unusual sensations.

On 13 February 1962, 15 additional events were recorded. The observatory had been alerted to expect these events; and so, *while they were recording,* the staff phoned about six of the Hilo residents who had reported alarming sensations during the morning of 20 December 1961. Of those called, only one thought that a similar event had just taken place, although no concern or alarm was engendered. This third
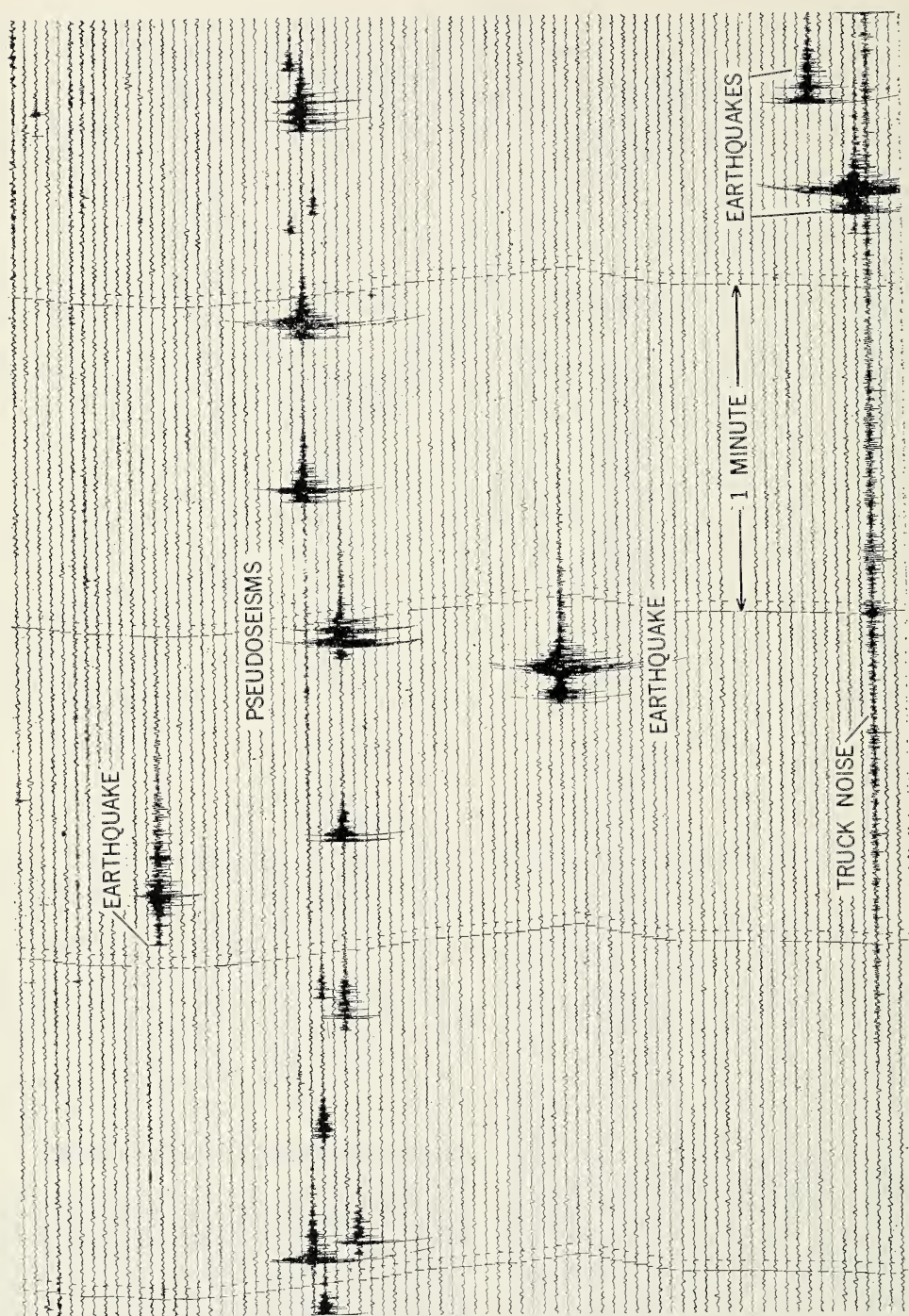
FIG. 2. Copy of original Desert seismogram showing events described in text.
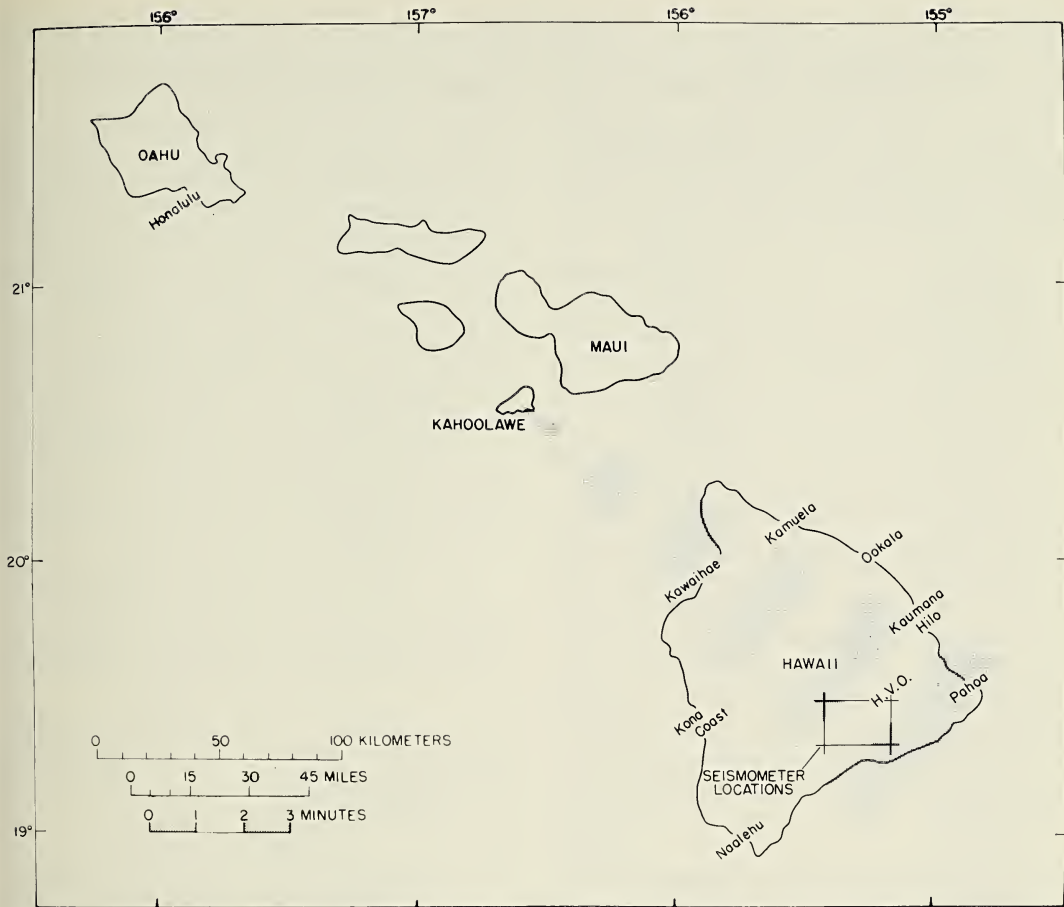
FIG. 3.   State of Hawaii east of Oahu, showing locales discussed in the text. The area enlarged in Figure 1 is outlined herein. Stipples indicate direction and travel time of advancing wave front.

series of events was recorded between 18:03 and 20:25 and most people who were called were watching television. A fourth series was recorded on 29 October 1963. It was sensed at the summit of Kilauea, but no calls were received from other places.

The third and fourth series of events presented a picture quite like the first two and have been only summarized in this presentation. Average differences between arrival times at Mauna Loa and at each of the other stations, for each of the four series of disturbances, are presented in Table 3.

The fourth column of Table 3 corresponds to the fourth series (of five events) which was confirmed to be sonic in nature but was not recorded at Mauna Loa. Relative arrival times of the 29 October 1963 series at Desert,

Uwekahuna, and Ahua are similar to those of the three earlier series.

ORIGIN OF THE DISTURBANCES

After the first series of disturbances on 19 and 20 December 1961, it was ascertained that Navy bombing exercises had been conducted during the suspect time-intervals. The target islands Kahoolawe and Kaula Rock had been "dive bombed" by aircraft from the carrier USS "Coral Sea," using 500- and 1,000-lb bombs which exploded on contact (rather than above or within the ground). Figure 3 shows the Hawaiian Islands east of Oahu and indicates sectors of airspace traversed during successive 1-minute intervals by sonic wave fronts which originated at Kahoolawe. The region on Hawaii

TABLE 2

MATCHED ARRIVAL TIMES AT SUMMIT STATIONS OF THE EVENTS OF 20 DECEMBER 1961
(Numbers in parentheses are recorded double-amplitudes, in millimeters)

DESERT	UWEKAHUNA	AHUA	MAUNA LOA
09-56-42.5(21)	43.7(4)	57-00.9(5)	06.5(5/2)
10-26-56.6(14)	56.2(4)	27-12.9(6)	19.3(3/2)
27-15.5(3)			
27-45.0(13)	45.0(4)	28-02.0(4)	08.0(2)
29-18.8(24)	19.5(4)	36.2(3)	28-42.8(1)
30-03.0(3/2)			
30-48.9(14)	51.0(5)	31-08.0(3)	14.5(2)
31-52.0(5)	52.0(2)		
11-11-07.3(6)	07.5(4)	27.5(3)	10-29.5(1)
40-54.7(12)	56.0(6)	41-12.0(1)	16.8(1)
41-23.3(17)	23.0(7)	41-40.5(1)	40-46.3(3/2)
41-44.8(17)	44.1(6)	42-02.3(2)	07.0(3)
42-12.9(16)	13.1(3)	30.7(3)	36.3(2)
47-40.6(5)	41.6(4)	57.9(2)	04.6(5/2)
48-40.9(20)	41.5(2)	59.1(1)	04.8(1)
49-04.2(16)	05.1(7)	21.3(2)	
49-33.0(12)	34.6(11)	51.6(7)	48-57.6(2)
53-27.5(11)	27.8(2)		
54-19.0(15)	19.5(4)	36.4(3)	53-42.9(3)
54-38.2(10)	38.6(2)	55.9(1)	01.8(1)
55-12.0(4)			
59-52.8(9)			
12-00-45.8(20)		01-03.5(6)	09.5(1)
01-12.0(14)			00-36.1(1/2)
06-31.0(11)	31.2(2)	49.5(2)	05-53.0(3/2)
07-28.0(5)		46.3(1)	
07-32.2(4)			
08-02.5(4)			
11-44.5(21)	45.0(3)	12-03.0(5)	08.8(3)
12-44.4(20)		13-02.5(1)	08.6(3/2)
19-40.8(23)	41.8(8)	58.9(19)	04.7(3/2)
27-54.3(17)	52.2(2)	58-10.0(3)	16.2(3)
59-26.0(14)	26.7(3)	43.8(8)	58-49.6(5)
13-01-12.5(18)	13.7(9)	30.7(9)	00-36.6(4)
04-27.7(18)	28.7(7)	45.9(2)	03-51.7(2)
05-46.5(31)	47.5(6)	06-04.2(4)	10.1(6)
06-42.7(13)	43.1(3)	07-00.6(2)	06.3(1)
11-17.6(21)	18.6(6)	35.8(6)	10-41.2(4)
12-02.9(15)	03.8(3/2)	21.1(5/2)	11-26.6(7)
13-03.6(9)	04.6(2)	21.5(1)	12-27.5(3)

TABLE 3

TIME OF ARRIVAL OF SONIC WAVE FRONTS AT EACH STATION COMPARED WITH
ARRIVAL AT MAUNA LOA, FOR EACH OF FOUR DIFFERENT BOMBING DATES

STATION	ORDER OF ARRIVAL	19 DEC. 1961	20 DEC. 1961	13 FEB. 1962	29 OCT. 1963
Mauna Loa	(1st)	0	0	0	not recorded
Desert	(2nd)	+35.9 sec	+36.4 sec	+36.6 sec	"+36.3 sec" (assumed)
Uwekahuna	(3rd)	+ 0.7 sec	+ 0.6 sec	+ 0.2 sec	— 0.2 sec
Ahua	(4th)	+16.9 sec	+17.2 sec	+16.7 sec	+16.7 sec

in which the disturbances were recorded and felt is approximately 190 km from the Kahoolawe source. Kaula Rock is 400 km to the west of Kahoolawe. An approximate schedule supplied by the Navy did not specify the exact time of any individual explosion or the total number of bombs dropped. By virtue of overlap in attack periods on the two islands, however, there is weak evidence, based on schedules of exercises for 19 and 20 December 1961, that all disturbances recorded and felt on the island of Hawaii originated at the closer target, Kahoolawe. On 13 February 1962, both targets were bombed simultaneously, but because the bombing log is skeletal, no conclusions can be drawn. No log was provided for the exercise of 29 October 1963; but it was confirmed that bombing had taken place and it was implied that only Kahoolawe was involved.

Bombing exercises on these targets during 1961 only, and qualitative results from them obtained by searching the seismograms follow:

DATE	HOURS	RESULTS
24 Feb.	06:40–14:30	No recordings, eruption tremor in progress. No sensations reported.
16 May	05:30–13:00	Neither recordings nor sensations.
22 Aug.	05:00–12:00	Same as above.
	15:30–20:00	Same as above.
23 Aug.	09:35–13:30	Same as above.
18 Nov.	05:40–13:10	Weakly recorded on Ahua only, no sensations reported.
20 Nov.	10:30–13:40	Neither recordings nor sensations.
	17:45–19:20	Weakly recorded on Ahua only, no sensations.
21 Nov.	09:30–13:35	Very weak on Mauna Loa and Ahua only, no "felt" reports.
19 Dec.	06:30–12:30	Weakly recorded, no sensations reported.
	17:45–20:00	Many reports and good records (Table 1).
20 Dec.	09:30–13:00	Some reports and good records (Table 2).

GRAPHICAL ANALYSIS: FIGURE 1

Because of the almost simultaneous arrival of the sonic waves at Uwekahuna and Desert, it was convenient to use a graphical technique to estimate the azimuth to the source on the basis of data summarized in Table 3. On Figure 1,

therefore, an assumed wave front has been drawn at the instant it passes Desert seismometer. The seismic stations which time such wave fronts are arrayed along a chord which is approximately 20 km long and about 20 km from the source. With this geometry, the chord is within 0.3 km of the circular segment it intersects; therefore, straight-line wave fronts have been assumed.

Seismograph recordings of sonic disturbances differ considerably from those of local earthquakes. There are no definite phase identifications for sonic arrivals as recorded by short-period seismometers; instead, the maxima have been read on each record. Some events were recorded as featureless bursts barely resolvable above the normal background noise. The Desert record as illustrated in Figure 2 usually gave the clearest and largest arrival. We can only speculate on the possible interference of wave groups following slightly different paths from the source to the receivers and on the effect such interference would have on the times of maxima at different receivers. However, the relatively low velocity of sound in air reduces the degree of precision necessary in timing sonic arrivals compared with that for seismic waves, for example.

If we assume that the correlation of the sonic arrival between receivers was in error by 5 or 10 seconds, and if we apply all of this error at either extreme of the hypothetical 20-km recording chord, errors of only 1° of arc would result. These errors are so small that confusing a source on Kahoolawe with one on Kaula Rock seems unlikely.

If we make these simplifications and allowances for error, and if we assume further that constant velocity prevailed in the seismic recording zone and over the 200-km propagation path, a direction of N 44°–46° W may be read from the diagram on Figure 1. This solution is excellent for a Kahoolawe source. (The Kaula Rock target is about N 64° W of the seismic pickup location.)

VARIATIONS IN APPARENT VELOCITY

The traveltimes (averaged from Table 3) for each leg in the wave front's passage are shown in Figure 1. The spacing provided by

existing instrument locations indicates two distinct travel paths: the high elevation path, from Mauna Loa to Desert/Uwekahuna, and the lower elevation path, from Desert/Uwekahuna to Ahua. Apparent velocity for the high elevation path is 0.33 km/sec, which, on the basis of the slope distance of 12.6 km, results in a ground velocity of 0.35 km/sec. These results are consistent with sonic velocities in air (Chemical Rubber Publishing Co., 1947:1928) of 0.33 km/sec at 0° C, and 0.34 km/sec at 20° C. Similarly, the lower elevation wave front path yields an apparent velocity of 0.37 km/sec, a condition observed at ambient temperatures of about 70° C.

Blumenstock (1961) summarized weather data collected in Hawaii and concluded that the winter mean temperature was 20° at the National Park housing area (see Figure 1) and that it decreased 2° for every 1,000 ft of elevation. He observed the remarkably "equable temperature conditions" in Hawaii—that is, the small range between winter and summer means at any one observation point—but he also stressed the great variations in temperature and in rainfall caused by very local topographic situations.

Additional, near-surface temperature variables which may bear on our present problem are the diurnal temperature and wind-direction patterns. In table 3, the 19 and 20 December 1961 figures represent average traveltimes for a large number of events in each of two groups. The 19 December events occurred at night; the 20 December events occurred during the daytime. The apparent velocities which occurred in the two events are:

(1) Mauna Loa to Desert (12.6 km slope distance): 35.9 sec, or 0.351 km/sec for the evening events; 36.4 sec, or 0.347 km/sec for the daytime events.

(2) Desert to Ahua (6.4 km distance): 17.6 sec, or 0.364 km/sec for the evening events; 17.8 sec, or 0.360 km/sec for the daytime events.

As shown above, the gross velocity increases as the sound front moves from the slopes of Mauna Loa to the flatter terrain at the summit and flank of Kilauea, and the velocities are systematically lower in the daytime than at night. At one atmosphere pressure, the velocity of sound in air increases 0.012 km/sec between 0° C and 20° C. Therefore, the natural expectation would be the reverse of our findings, i.e., velocities expectedly would be slightly greater during the daytime than during the evening, when temperatures are lower. Again, Blumenstock's findings (1961:6) can be invoked for a mechanism which might explain this seeming contradiction: "The usual regime is to have upslope winds by day and downslope winds by night." In our situation downslope winds (nighttime) would augment velocities across our recording range; upslope winds (daytime) would provide relative decreases in apparent velocities. The velocity increase we seek to explain by this mechanism is 4 m/sec or about 8 miles/hr—a modest windspeed vector which is not unrealistic.

Thus, some of the diurnal changes in sonic traveltime shown in Table 3 can be explained by assumptions of expectable change due to diurnal wind-velocity conditions. However, such changes can be only partially responsible for the difference between apparent velocity over the Mauna Loa-to-Desert leg and that over the Desert-to-Ahua leg. As we have pointed out, such an assumption would require an unrealistic ambient temperature of 70° C for the low-elevation, high-velocity segment.

ANGLE OF INCIDENCE OVER THE
RECORDING RANGE

It has been demonstrated above that the sonic travel path from Mauna Loa station down to Desert and Uwekahuna fits into a reasonable model for sound-wave rays moving parallel to the ground across that particular path. By contrast, the lower elevation segment of the recording range—that between Desert and Ahua—offers evidence of increased velocity which cannot be explained by temperature alone. It might be explained by a favorable component of wind velocity, but that would require wind velocities in excess of 50 mph, a condition rarely observed in Hawaii. The best situation producing such a velocity increase, as well as one which would also provide for energy focusing, would be encountered if the sonic rays impinged upon the low-elevation stations at a steeper angle of incidence.

A plausible hypothetical model is therefore considered, and with vastly oversimplified parameters. At an ambient temperature of 20° C, which is given by Blumenstock as the winter mean for the Park housing area, sonic velocity is 0.345 km/sec. In fact, we observe a velocity of 0.37 km/sec for the range south and east of the housing area. If all of this excess is assumed to be due to incidence angle, it may be computed:

$\sin \alpha = .345 = 69°$, where α is the angle between the incident ray and the vertical.

Energy from Kahoolawe can then be imagined to impinge upon the Mauna Loa and Kilauea recording range as follows: On the slopes of Mauna Loa, wave fronts move downhill and are normal to the surface of the ground; on the flatter, low-elevation terrain, wave fronts are about 20° from the vertical. Such increases in the angle of incidence would improve coupling between air and ground, and if such improvement occurs as theorized above, the maximization of available energy and "seismic" manifestations reported by residents would be the expected results.

THE GROSS PROPAGATION PATH

The many uncertainties discussed for the limited region of acoustic recording are clearly multiplied in a consideration of the size and complexity of the air space through which the energy is refracted. At present there are few concentrated data which describe atmospheric conditions over Hawaii. For example, although daily weather observations are made at Hilo, these are limited to that place and concern only operational altitudes for aircraft.

Perkins et al. (1960) illustrated many theoretical and actual instances of the focusing of sonic energy due to meteorological conditions. Their work seemed to involve more limited source-to-target distances; on their computed graphs data are restricted to areas having a maximum altitude of 10,000 ft and to lateral distances of about 100,000 ft. Variables discussed in that report were those of temperature and wind velocity; the stratification thus produced caused favorable refracting conditions and, in turn, focusing. Such conditions in

Hawaii are known only generally, but salient features which would be propitious in generating the special phenomena we have recorded are summarized:

(1) Wind velocities which increase with altitude in the Hawaii direction from Kahoolawe. This condition is prevalent in the winter when trade winds (blowing westward) abate and counter trade winds blow near the ground. Thus, the propagation pattern discussed above would be enhanced during the Hawaiian winter and it would normally be inoperative during the rest of the year.

(2) High velocity (higher temperature) propagation paths which serve to refract energy in the Hawaii direction. This condition prevails most of the time (Blumenstock, 1961) in the form of a sharp temperature inversion overlying the Hawaiian area at altitudes between 5,000 and 7,000 ft.

(3) Jet streams in a sheath above 40,000 ft, the least understood, but an important, feature. These jets, which supposedly blow toward the east (thus contributing to situation (1), above), can make radical changes in direction and can attain great velocities.

Although more accurate information about possible zoning or velocity/temperature stratification between Kahoolawe and Kilauea would be helpful, it is still possible to come up with an approximation suggested by Perkins et al. (1960), who suggested a single gradient case. This oversimplification would call for Kahoolawe and Uwekahuna to lie at opposite ends of a chord connecting them. The chord, therefore, would be 190 km in length. And the circular path intersected by this chord would describe the simplified refracted energy path. If it is further assumed that tangents to this circular path at either end make an angle of 20° with the (horizontal) chord (i.e., if we interject the previously computed angle of incidence), a circular path 280 km in radius results. Such a path would reach a height of 17 km before refracting downward. This suggestion of a major refracting condition somewhere near an altitude of 55,000 ft is in good agreement with available knowledge about the altitude of the tropopause over Hawaii (described briefly in (3) above).

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Gravity and Geological Studies of an Ultramafic Mass in New Zealand[1]

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ABSTRACT: A gravity and geologic survey was carried out over a portion of the Nelson ultramafic belt of the South Island. In this region, the ultramafic rocks out-crop over a 5-mile-wide belt and abut against the Alpine greywacke along the right lateral transcurrent Alpine Fault. The dunite and peridotite of the ultramafic belt as well as the overlying geosynclinal sediments strike north. At their southern ex-tremity, these rocks are faulted by the northeast–southwest striking Alpine Fault against the massive Alpine greywackes to the south of the fault. There is a com-plete discordance of the stratigraphic elements between the two sides of the fault. The basal Permian ultramafic belt (Wairau ultramafic mass) to the north of the fault is horizontally layered and shows inch-scale layering comparable to that ob-served by Hess in the Stillwater complex of Montana. Stratigraphically above the Wairau ultramafic mass and also on the northern side of the fault lies a vertically dipping, 31,000-ft-thick sequence of serpentinite, spilite, grey slate, red and green slate, and tuffaceous sandstone. The density of the rocks surrounding the Wairau ultramafic mass varies between 2.65 gm/cc and 2.75 gm/cc, while that of the peridotite and dunite varies between 3.2 gm/cc and 3.3 gm/cc. A total thickness of 7,000 ft for the Wairau ultramafic mass was computed, using the average den-sity contrast of 0.5 gm/cc between the ultramafics and the country rock. Gravity analysis also shows that the Alpine Fault dips 67° southeast along the contact between the ultramafics and the Alpine greywacke.

It is thought that the Wairau ultramafic mass was emplaced as a vertical dike when the surrounding rocks were horizontal and that the dike and the surrounding rocks have been rotated by 90° so that the dike is now horizontal and the beds are vertical. Comparisons between the stratigraphic sequence studied here and an almost identical sequence on the southern side of the Alpine Fault in Otago province supports the previously postulated 300-mile-long transcurrent displacement between the two areas along the Alpine Fault system of New Zealand. Studies of displace-ment of post-glacial river terraces along the Alpine Fault in Nelson show an average right lateral movement of 0.36 inches per year along the fault since the last glacia-tion.

THE ORIGIN of emplacement of ultramafic rocks has always been a prime geologic problem in world geology. There are two ultramafic belts in New Zealand and these are separated by a 300-mile-long displacement along the Alpine Fault system of New Zealand. The New Zea-land ultramafic belts have an added interest be-cause of this prominent fault movement. They provide an accessible source for geophysical and geological investigation, in the country where dunite was first described.

Of particular interest to the geophysicist and geologist alike are the two areas where the ultramafic rocks abut against the fault planes of the Alpine Fault. In these regions, a genuine physical cross section is obtained across the ul-tramafic rocks and their associated formations where the Alpine Fault system has cut across the formations.

One of these two regions is located in South Nelson in the northern part of the South Island of New Zealand and has been named, in this paper, the Tophouse district. A reconnaissance geological survey was carried out by the author

in 1961–1962 over the Tophouse district in order to map the geologic boundaries of the ultramafic belt and all visible fault traces of the Alpine Fault system. Another purpose of the geological survey was to compare the lithology, structure, and thickness of the geologic formations in the Tophouse district immediately north of the Wairau Fault with similar formations south of the Alpine Fault in Otago, 300 miles southwest of the Tophouse district.

A gravity survey was carried out simultaneously with the geological survey over the Tophouse district in order to map the maximum thickness of the ultramafic rocks, and their attitude as they abut against the Wairau Fault, and to investigate whether there is any subsurface extension of the ultramafic belt south of the fault in the Tophouse district. Gravity surveying appears to be one of the best geophysical methods to use in the study of ultramafic belts because of the high density contrast usually measured between the peridotite and the country rock into which the peridotite has been intruded.

It is hoped that this paper will serve as a useful contribution to the gravimetric study of ultramafic rocks throughout the world.

GEOLOGY

Outline of Stratigraphy

The rocks of the Tophouse district (Fig. 1 and Table 1) consist of two classes, pre-Tertiary rocks and extensive post-glacial deposits. The pre-Tertiary rocks are divided into three fault blocks (Fig. 2): (1) the Brook Street volcanics west of the Waimea Fault and probably underlain by rocks of the Rotoroa igneous complex; (2) the Maitai and Te Anau series, east of the Waimea Fault and north of the Wairau Fault; and (3) the Alpine greywacke, south of the Wairau Fault.

The relationship between the rocks of the Tophouse district and those of the ultramafic belt in Otago south of the Alpine Fault is shown in Table 2.

Outline of Structure

The Wairau Fault, the major one of the district, is a right lateral fault downthrown to the north. It is probably a branch of the Alpine Fault, together with which it forms a 300-mile-long transcurrent fault system which separates the Maitai and Te Anau rocks of the Tophouse district from those of Otago (Wellman, 1956:25).

The strike of the Brook Street volcanics has changed as a result of stresses associated with movement along the Wairau Fault. At Tophouse, the Brook Street volcanics strike at 360°, i.e., parallel to the Waimea Fault. At Lake Rotoiti, these volcanics have been regionally bent to strike at 60° and fault swarms have developed at intermediate angles between the strike of the Waimea and Wairau faults. The Waimea Fault has not been active during the post-glacial period.

The Maitai and Te Anau formations have undergone strike-faulting, but the Wairau ultramafic mass shows little sign of structural deformation. Detailed geology of the Tophouse district is shown on the geological map, Figure 2, and the stratigraphic units are presented in Table 1.

Brook Street Volcanics

The Brook Street volcanics of the Te Anau series are part of the southern end of a sequence of Upper Paleozoic volcanics which extend from d'Urville Island to Tophouse. The continuous Waimea Fault between the Brook Street volcanics and the Maitai series makes stratigraphic relationship at Tophouse uncertain. No fossils were found in the Brook Street volcanics in the Tophouse district; however, they are considered Upper Paleozoic here, the age assigned by Bruce (1962:166) to the Brook Street volcanics of Nelson.

The bulk of the rocks are massive metasomatized spilites and green-grey keratophyres. Along the Waimea Fault, there is an outcrop of a green volcanic conglomerate. The spilites are dense, hard and nonvesicular. The dip of the volcanics has been determined from alignment of xenoliths and mineral grains. The spilite exposed in the Motupiko Valley is equigranular and fine grained, with 20% subcalcic augite (2V = 20°) and with 60% plagioclase feldspar. The augite crystals are corroded and set in a highly altered groundmass of epidote and chlorite. The green color of the Brook Street volcanics results from the alteration of mafic minerals to chlorite.

FIG. 1. Rock types north of the Tophouse district. Inset shows geographic location of Tophouse district.

FIG. 2. Geology of the Tophouse district.

Map labels (within figure):

Yg · Yg · 635 · Ers · Ers · Er · 640
Eβ · Er · Ers
↙70 · ×50 The Plateau · Es
↙80 · Yrλ · 70↙80 · Eβ · T 65
↙70 · Yr · Eγ · Ers
Beebys Creek · Yg · 75 · Eβ · F · Eε · 775
↙80 · Yrλ Es · 70↙ · Eβ · Ers · T · H
↙80 · Yg · 70↙ · H
Yr · Es · H
↙↙↙80 · ↙80 · Maitland Fault · River · H · T
↙70 · ↙71 · ↙72 · H
Yg · West Coast–Blenheim Hwy. · Wairau · T
F · T
T · T
H · H
Yg · H · W
m · T
T · H
Wairau · River · T
H

BEDDING
✗ Inclined
✗ Vertical

〜〜 Distinct boundary
– – – Indistinct boundary
F Faults
——— Faults recently active

Cenozoic covering strata

LITHOLOGY

H	Post-glacial river deposits
S	Greywacke scree
Tm	Uplifted Pleistocene gravels (Tophouse gravels) covered by moraine in places (approximate boundary only)

Paleozoic and Lower Mesozoic rocks

FORMATION, GROUP		SYSTEM, SERIES	PERIOD
Ys	Stevens Formation siltstone, sandstone, congl.		
Yw	Waiua Formation red and green argillite	Maitai series	Lower Permian
Yg	Greyville Formation grey banded ms. and ss.		
Yrλ	White hard limestone	Rangitoto F.	
Yr	Calcareous sandstone		
Es	Spilite, dolerite		
EB	Red and green volcanic breccia		
Eβ	Serpentinite		
Eγ	Dunite, peridotite	Wairau Ultramafics Mass	Te Anau series	Basal Permian
Eγs	Dunite scree, dunite		
Eδ	Hydrogrossula in serpentine		
Eε	Rodingite Amphibolite		

Rocks west of Waimea Fault

| B | Brook Street Volcanics | | (?)Carboniferous |

Rocks south of Wairau Fault

| R-W | R Mt. Robert Group W Raglan Group Greywacke | Alpine Facies | (?)Triassic |

FIG. 2. Geology of the Tophouse district.

Cenozoic covering strata

LITHOLOGY

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Eβ	Red and green volcanic breccia		
Eβ	Serpentinite		
Eγ	Dunite, peridotite	Woirau Ultramafics Moss	Te Anau series	Basal Permian
Eγs	Dunite scree, dunite		
Eδ	Hydrogrossula in serpentine		
Eє	Rodingite Amphibolite		

Rocks west of Waimea Fault

| B | Breok Street Volcanics | | (?)Carboniferous |

Rocks south of Woirou Fault

| R W | R Mt. Robert Group W Raglan Group Greywacke | Alpine Facies | (?)Triassic |

BEDDING

⅄ Inclined
✕ Vertical

〰 Distinct boundary
- - - Indistinct boundary
F Foults
— Foults recently octive

Grid is the N.Z. national one thousand yard grid

0   1   2
MILES

Prospector's Creek
Beebys Creek
Morupito River
Rainy River
Butler River
St. Arnaud River
Wairau River
West Coast Blenheim Hwy
Woirau River
Waimea Fault
Maitland Fault
Wairau Fault
Glacial moraine boundary
The Plateau
Loke Roto-iti

Lionel Medeiros

TABLE 1

STRATIGRAPHIC UNITS OF THE TOPHOUSE DISTRICT

SERIES AND AGE	FORMATION	MAP SYMBOL	LITHOLOGY	MAXIMUM THICKNESS IN FEET*
		S	mountain scree	
	Wairau surface	H	gravels, 10-ft terrace	100?
Holocene	Tophouse surface	T	fluvial gravels, silts, 200-ft terrace	300?
		Tm	glacial moraine	200?
		Major Unconformity		
Tertiary		t	terrestrial sediments	600?
		Major Unconformity		
	Stevens formation	YSa	tuffaceous siltstone (5,000 ft thick)	
		YSb	tuffaceous sandstone (6,000 ft thick)	11,000
Maitai Series,	Waiua formation	Yw	green and purple banded mudstone and sandstone	2,500
Upper	Greville formation	YG	grey banded argillite	9,000
Permian (?)	Rangitoto formation	YRλ	white limestone (2,000 ft thick)	
		YR	grey calcareous sandstone (1,800 ft thick)	3,800
		Cessation of Igneous Activity		
		Es	spilite, dolerite (extensively haematized)	4,000
		EB	haematized red and green volcanic breccia	1,000
Te Anau Series,		Stratigraphic Relationship Uncertain		
Basal Permian		Eβ	serpentinite	2,000
		Eγ	dunite, harzburgite, pyroxene peridotite	7,000
	Wairau ultramafic	Eγs	peridotite and peridotite scree	
	mass	Eδ	serpentine containing hydrogrossular	500
		Eε	amphibolite, rodingite	5,000?
Rocks West of the Waimea Fault				
Te Anau Series, Carbonif- erous (?)	Brook Street volcanics	B	keratophyre, andesite, volcanic agglomerate, spilite	12,000
Rocks Southeast of the Wairau Fault				
Triassic	Alpine facies	R	Mount Robert group— greywacke, argillite	?
		W	Raglan group— greywacke, argillite	?

* As measured across outcrops in the Tophouse district.

TABLE 2

STRATIGRAPHIC CORRELATION BETWEEN PERMIAN ROCKS OF OTAGO* AND THE TOPHOUSE DISTRICT

SERIES AND AGE	FORMATION	EQUIVALENT TOP-HOUSE FORMATION	LITHOLOGY	THICKNESS IN FEET
Maitai Series, Upper Permian?	Countess formation	Stevens formation	green, grey, maroon bedded sandstone, grit, conglomerate	11,000+
	Winton formation	Waiua formation	red- and green-banded argillite	1,000
	Tapara formation	Greville formation	grey-banded argillite	7,000
	Howden formation	Rangitoto formation	grey Maitaia bioclastic limestone, green sandstone, conglomerate	2,000
Cessation of igneous activity but no break in sedimentation				
Te Anau Series, Basal Permian	Livingstone volcanics		spilite, albite dolerite, albite gabbro, epidiorite, red and green breccia	3,000
	Red Mountain ultramafics	Wairau ultramafic mass	peridotite, dunite, serpentinite, gabbro, rodingite	?
Stratigraphic relationship unknown				
	Eglinton volcanics		andesite, basalt, porphyrite, keratophyre, breccia, tuff	?

* From stratigraphic sequence determined by G. W. Grindley, 1958.

Volcanic conglomerate outcrops east of the Motupiko River and consists of rounded spilitic pebbles up to 3 cm in diameter, set in a chloritic groundmass (VUW 10658).[2] Phenocrysts of oligoclase feldspar are partially altered to epidote and seracite. The volcanic conglomerate is faulted against Stevens formation (Maitai series) by the Waimea Fault.

Te Anau Series

Grindley (1958:22) defined the Te Anau series in Otago as Upper Paleozoic (post-Devonian) sediments, volcanics, and intrusives deposited or erupted prior to the deposition of the Lower Permian Maitai limestone and not subsequently converted into schist or gneiss. In the Tophouse district, the Te Anau series is represented by the Wairau ultramafic mass and the Te Anau volcanics and underlies the Maitai limestone.

Wairau Ultramafic Mass

This mass is one of the two unserpentinized ultramafic masses of the Nelson ultramafic belt (see Fig. 1). A similar belt of ultramafic rocks extends southeastward from the Alpine Fault in Otago. The Red Mountain ultramafics of Otago (Grindley, 1958) are similar mineralogically to the Wairau ultramafic mass of South Nelson.

The rocks of this mass consist of peridotite and serpentinite. The largest exposure of peridotite is at the "Plateau," a peneplain surface 2,400 ft above the Wairau Valley. Northward of the Plateau, the peridotite becomes progressively dissected, resulting in craggy crests and steep, scree-covered slopes. While the Maitai rocks and Te Anau volcanics are covered by beech forest and scrub, the ultramafic rocks are covered by tussock grass only.

The Wairau ultramafic mass is faulted to the south, west, and possibly to the east. Air photographs show a strong lineation at 57° which is due to the alignment of dikes composed principally of pyroxenite. Banding, similar to that described by Hess (1960) in the Stillwater complex of Montana, is found along the whole western edge of the ultramafic mass. The coarse bands, consisting of pyroxenite and varying

from 1 to 2 cm in width, are repeated hundreds of times within any outcrop. The dip in the area mapped is relatively low, from 20° to 40° E. The relationship of the banding to the general lineation referred to above is complex, and was not studied in detail.

The rocks of the Plateau include dunite, ortho- and clinopyroxene peridotite and harzburgite. These rocks are dark green and coarse-grained, and contain crystals up to 0.5 cm in diameter. Bands of resistant orthopyroxenite frequently stand out on the surface of the weathered rock. The pyroxene in the peridotite varies in type. Chromite is the sole accessory mineral. The dunite consists of large interlocking crystals of olivine, showing "strain" lamellae, and accessory chromite which occurs as elongate crystals, 2 mm in length. The density of the peridotites is constant at 3.30 ± 0.05 gm/cc for fresh unserpentinized samples and provides the density contrast of 0.6 gm/cc between the peridotites and New Zealand greywacke (the basement rock of 2.70 gm/cc density which is assumed to underlie the peridotite).

Serpentine containing hydrogrossular outcrops in the center of the Plateau and is coarse-grained, dark blue, and massive. Hydrogrossular is set within mesh serpentine in the rock, and olivine relics as well as diopside fragments are abundant. The rock contains 10% granular magnetite. The gradational nature of the contact between the serpentinite and the surrounding peridotite suggests a metasomatic origin for the serpentinite.

Crushed serpentinite outcrops along a belt west of the Maitland Fault and forms the western boundary of the Wairau ultramafic mass. The Maitland Fault is the boundary between this serpentinite and the undeformed peridotite of the Plateau. The serpentinite is light green in color and breaks readily into green lensoid fragments 5–10 cm in diameter and 1–3 cm in thickness. Rocks near the Maitland Fault consist of antigorite serpentinite with slip fiber structure and are composed of large tabular crystals of antigorite with minor diopside. Tabular crystals of magnetite 2.5 mm in diameter form at least 10% of the rock by weight.

Amphibolite and rodingite occur as a wedge in the northeast corner of the area mapped (Fig.

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[2] These numbers refer to rock catalogue numbers of specimens stored in the Geology Department, Victoria University of Wellington, New Zealand.

2) and appear to be faulted against the ultra-mafic rocks. Dikes of dense, white, fine-grained grossular diopside and chlorite rodingites (Grange, 1927) outcrop in stream beds of the Red Hills. The amphibolite which also outcrops in the same area is dark grey in the hand specimen and equigranular with aligned green hornblende crystals.

Upper Te Anau Volcanics

The breccia, spilite, and dolerite of the Tophouse district are similar to those in the belt of volcanics (Livingstone volcanics) between the Red Mountain ultramafics and the Howden formation of the Hollyford and Pyke Valleys in Otago (Table 2). The belt is cut off at the head of Pyke Valley by the Alpine Fault. In both Otago and South Nelson, the volcanics outcrop immediately above the serpentinite of the ultramafic belts and immediately below the Maitai limestone.

Distinctive red and green volcanic breccia outcrops immediately west of the Wairau ultramafic mass and is in direct contact with the serpentinites. The breccia consists of sub-angular fragments of spilite and dolerite pebbles, up to 15 cm in diameter but averaging 2 cm, surrounded by an igneous reaction rim. The pebbles are set in a fine-grained, dark-red hematitic base with vugs of calcite, and magnetite relicts. The breccia band is only 1,000 ft wide, dips steeply east, and strikes at 330°. To the east, the breccia is in direct contact with the serpentinites.

A belt of spilite, cut by dolerite dikes, lies between the breccia and the Maitai limestone. Directly beneath the limestone, the spilite is hematized and, in thin section (VUW 10667), shows vugs filled with spherulites of quartz and chlorite as well as phenocrysts of augite and serpentinized olivine set in a hematitic base. In the groundmass, acicular pyroxene crystals are aligned parallel to igneous flow structures. Magnetite, originally abundant, has been changed to hematite, giving the rock a red coloring. Away from the limestone contact, the spilites are green-grey in color. Texture is non-vesicular with a medium grain size.

Maitai Series (Group)

The lower formation of this series is the Maitai limestone in both the Tophouse district and in West Otago. The upper formation in these districts consists of volcanically derived sandstone. The four formations in the Maitai series in the Tophouse district may be correlated with those of Nelson and those of Otago (Grindley, 1958), which they match closely (Table 2). The oldest formation is Lower Permian in age (Wellman, 1952) and the youngest formation is Upper Permian. The Maitai formations have distinctive lithology and are easily mapped.

Rangitoto Formation

The formation is 3,800 ft thick and is well exposed along hill crests, west of the Red Hills. The base is marked by grey calcareous sandstone (30–40% calcite) with casts of *Atomodesma* impressions. The rocks show slaty cleavage and dip steeply east. The strike varies from 345° near the Wairau Fault to 025° two miles north. The calcareous sandstone grades up into coarse-grained massive limestone which in turn has a gradational contact with the Greville formation.

Greville Formation

The Greville formation consists wholly of laminated grey argillite and is exposed in a continuous sequence about 9,000 ft thick. Banding is regular, between 0.1 and 0.2 inches thick, and similar to that of varves. The darker bands consist of graded, coarse sandstone and lighter bands of fine siltstone. Slaty cleavage is well developed in parts of the formation. The strike of the rock is 015° and the dip ranges from 80° to 100°. Strike faulting is prominent and much of the drainage over the formation is aligned with the strike direction.

Laminations are graded, but much thinner than graded bands in greywacke. The resemblance between the laminations of the Greville argillites and those of varves shows up even more clearly under the microscope than in the hand specimen. It is likely that the bands represent annual layers.

Waiua Formation

The Waiua formation occurs as a faulted inlier near the Tophouse Hotel, where 2,500 ft of the rock is exposed. The rock consists of red- and green-banded argillite and sandstone with

well-developed cleavage. The strike is 340° and the dip is nearly vertical. The banding in the argillite consists of tuffaceous sandstone, 3 mm thick, interbedded with argillaceous laminations 0.5–1.5 mm thick. In thin section, the green bands are seen to consist of sandstone with elongate grains of pyroxene, feldspar, and magnetite, set in a chloritic base. The red bands consist of argillite with a large proportion of hematite. Augen of hematite also occur in the sandstone bands. All the layers show graded bedding with laminations similar to those of the Greville formation. At the top of the formation, spacing of bands is irregular and thicker than in the Greville formation, massive semibanded silts (VUW 10663) becoming prominent. Tuffaceous, banded sediments near the top of the formation consist of oligoclase feldspar, pyroxene, epidote, chlorite, and magnetite. All mineral grains show rounding. Green volcanic tuffs (VUW 10662), massive or vesicular in hand specimens, appear near the top of the Waiua formation. The change in coloration from the uniform grey of the Greville formation to the red and green of the Waiua formation is attributed to a mixture of tuffaceous material.

Stevens Formation

The lower part of Stevens formation consists predominantly of massive, green, volcanic sandstone and the upper part of tuffaceous siltstone. The contact between the upper and lower parts is abrupt and is probably a fault. The sandstone is 6,000 ft thick and dips vertically. The siltstone is 5,000 ft thick and dips 60° E at 340°. The sandstone is hard, lacks cleavage planes, is resistant to erosion, and forms prominent hill crests. It consists of semirounded mineral grains 0.03 mm in diameter, set in a chloritic matrix. Pyroxene and epidote are the chief components and the green color of the rock is due to alteration products of pyroxene. The siltstone is exposed in stream beds northeast of Tophouse Hotel. In thin section (VUW 10660), it appears to have an arkosic (oligoclase feldspar) composition and a chloritic matrix.

Alpine Greywacke

Lower Mesozoic greywacke and argillite is exposed southeast of the Wairau Fault in the Tophouse district. No detailed study was made of these rocks, but the following points were noted:

a.) Greywacke southwest of Mt. Robert tends to be schistose and denser than 2.67 gm/cc.

b.) The rocks of Mt. Robert and the St. Arnaud Range consist of 40% sandstone and 60% argillite. The argillite is dark blue in color, shows well-developed cleavage, and is calcareous with prominent calcite veins.

c.) The rocks of the Raglan Range consist of 10–20% argillite and 80–90% sandstone. The sandstone is light-colored and hard, and consists predominantly of rounded quartz grains.

d.) Intraformational calcitic and hematized spilites (VUW 10685) are interbedded in the greywacke of the Raglan Range and the St. Arnaud Range.

Quaternary Deposits

Most of the Quarternary alluvial deposits in the Tophouse district represent glacial advance during the Pleistocene glaciation.

The Tophouse gravels were deposited during the first recognized advance. The glaciers flowed from the site now occupied by Lake Rotoiti and, overriding the Brook Street volcanics, flowed north along the Motupiko Valley. A branch glacier probably flowed west over the Tophouse saddle and descended 2–5 miles down the Wairau Valley (Henderson, 1931:156). The lower limits of the glaciers were at 1,500–1,800 ft above the present sea level.

The Wairau Fault

The Wairau Fault is the major tectonic feature in the Tophouse district and is probably an eastward extension of the Alpine Fault (Fig. 1). The fault was examined in the field, but most of the information was obtained from air photographs and is shown in Table 3 (with nomenclature adapted from Wellman, 1953) and plotted on the geological map (Fig. 2).

The fault strikes eastward from Lake Rotoiti. Minor branch faults occur near Lake Rotoiti and along the northwest side of the Wairau Valley. Displaced and fault-aligned streams mark the fault trace on the north slopes of the St. Arnaud Range. The dip of the Wairau

TABLE 3

DATA ON THE POST-GLACIAL MOVEMENT OF THE WAIRAU FAULT FROM SPEARGRASS CREEK, MT. ROBERT TO WASH BRIDGE IN THE WAIRAU VALLEY

NATURE OF FAULT TRACE	LENGTH IN MILES	STRIKE DIR.	DIP AMT.	DIP DIR.	VERTICAL THROW THROWN SIDE	VERTICAL THROW AMT. (FT)	HORIZONTAL THROW NATURE	HORIZONTAL THROW AMT. (FT)	REFERENCE SURFACE
Stream bed	2.0	52°			SE				Speargrass Creek along fault zone (?)
*Scarp	0.5	66°			SE				scarp, partly concealed by scree at base of Mt. Robert
Scarp	0.4	68°	75°	NW	SE	40	C†	300	displaced shore line and glacial moraine
*Scarp	0.4	68°	75°	NW	SE	40	C	300	displaced shore line
Scarp	0.5	55°	90°	—	SE	50			displaced terrace
Scarp	0.1	55°?	90°	—	SE	20			displaced terrace
Rent	0.1	64°	90°	—	SE	20	C	330	displaced shore line
*Scarp	1.0	63°	80°	NW	SE				truncated spur
Scarp	1.0	64°	80°	NW	SE	60			stream
*Scarp	3.0	64°	80°	NW	SE	50			displaced mountain spur
Rent	3.0	64°	90°	—			C	700	displaced mountain spur and displaced stream
*Rent	0.5	64°	90°	—	SE	30	C	300?	fault line crosses highway
Rent	0.5	68°	90°	—	SE	40	C	(?)	displaced terrace
Rent	0.2	67°	90°	—	SE	10	C	(?)	valley floor
Rent	0.3	67°	90°	NW	SE	80	—	—	gravel terrace
Rent	0.2	65°	85°	—	SE		—	—	displaced terrace
Rent	0.2	66°	90°	—	SE	10	—	—	displaced terrace
Rent	0.5	66°	90°	—	SE		—	—	recent movement (fault pond)
Scarp	1.0	42°	80°	SE	NW	200?	—	—	ancient fault trace
Scarplet	0.3	63°	85°	NW	SE	8	—	—	displaced terrace

* As determined by H. W. Wellman, 1952.
† C = Right lateral displacement.

Fault, as observed from surface scarps, appears to be vertical.

The ratio of the vertical to horizontal throw of the fault since the last glaciation is 1:10 (Table 4), and the rate of horizontal movement (including steady and sudden movement) is 0.36 inches per year. This rate is similar to the rate of 0.5 inches per year of dextral transcurrent creep recorded on the San Andreas Fault in California (Whitten et al., 1960).

TABLE 4

MEAN VALUES FOR VERTICAL AND HORIZONTAL
THROW OF THE WAIRAU FAULT

LOCALITY	VERTICAL THROW (FT)	HORIZONTAL THROW (FT)
L. Rotoiti Peninsula	40	300
East shore L. Rotoiti	20	330
North flank St. Arnaud Range	50	250
Blenheim- West Coast Highway	30	300
Mean Values	35	300

GRAVITY

In the Tophouse district, intrusive and sedimentary rocks of the Maitai series, the Te Anau series, and the Brook Street volcanics are faulted against the homogenous Alpine greywacke by the Wairau Fault. In order to provide a simple geologic model for the gravity studies, the density of each formation has been assumed to be uniform throughout and in depth. Lithologic boundaries have been of prime importance in the interpretation of the gravity data.

The Worden gravity meter (W283) used in the survey has a scale range of 800 divisions, each division having a value of 0.0971 mgal. The base map has a scale of ½ mile to the inch and was constructed by standard methods from air photographs. Heights were read at each gravity station with three altimeters and frequent checks were made to points of known height. Also, daily variations in air pressure were determined with a barograph, located at the base station. Drift of the gravity meter was corrected by beginning and ending a set of readings for one day at the same station.

Because of the practical difficulty of making terrain corrections in areas of irregular topography, station sites were chosen within areas of smooth topography.

Gravimetric Corrections

All Bouguer gravity values are given in terms of Glenhope-Christchurch, i.e., the New Zealand Provisional System (Robertson and Reilly, 1960). The following corrections were made to the "observed" values:

(1) Latitude correction: The 1930 International Formula was used for determining latitude corrections. The increase in gravity to the south of the Tophouse district is 1.493 mgal per minute of latitude, or 1.298 mgal per mile.

(2) Elevation corrections:

(a) Free-air correction: This correction is constant and is 0.09406 mgal per foot of elevation.

(b) Bouguer correction: The attraction of the rock (taken as an infinite sheet in all directions) per foot of elevation between sea level and the gravity station is 0.01276 times the density of the rock. The density is assumed to be 2.67 gm/cc (the standard rock density), and variations from the assumed density have been allowed for in the interpretation of the gravity profiles.

(c) The combined correction: The Bouguer and elevation corrections are combined and a correction of 0.05999 mgal per foot of elevation was used for all the gravity stations.

(3) Terrain correction: Hammer's tables (Hammer, 1939) and a graticule were used to allow for irregular topography, topographic data being obtained from direct observations out to 558 ft from the gravity station and from N.Z.M.S. 1 contoured topographic maps (S26, S27, S33, S34) from 558 ft to 14 miles.

Errors in the Gravity Values

The position of the gravity stations is known to about 100 yards. Latitude errors do not exceed 0.05 mgal and hence are negligible. Heights are accurate to about 10 ft and produce errors of about 0.6 mgal. Errors arising from the correction of topography (judging from local irregularities) in the observed values do not exceed 0.2 mgal. Errors caused by the drift

of the meter are negligible. The error in the Bouguer anomaly at any gravity station is not likely to exceed 1 mgal and is probably about 0.5 mgal.

Rock Densities

The density and magnetic susceptibility of representative rocks of the Tophouse district is given in Table 5.

In the Tophouse district, Maitai and Te Anau rocks are faulted against rocks of the Alpine facies whose measured densities range from 2.67 to 2.74 gm/cc and average 2.7 gm/cc. For the purposes of computation, the standard rock density for the Tophouse district is assumed to be 2.7 gm/cc, and differences from 2.7 are measured as the density contrast. Density differences between the standard rock and the overlying Maitai and Te Anau rocks are inferred to have produced the variations in the Bouguer anomalies (Fig. 3).

As the result of compaction and cementation, the porosities of most Maitai and Te Anau rocks are small. Only serpentinite and some tuffaceous rocks in the Maitai series have porosities greater than 5%. Fresh samples of Maitai and Te Anau rocks and of Alpine greywacke have porosities less than 2% and therefore particle densities have been adopted as the pre-

ferred density. Table 6 gives the particle densities of the Tophouse rocks and the density contrasts between these rocks and the local standard density of 2.7 gm/cc.

Gravity Anomalies of the Tophouse District

1. THE BOUGUER ANOMALIES: Dominant features of the Bouguer anomaly map (Fig. 3) are the northeast lineation of the anomaly contours and the decrease in gravity values southeast toward the regional low of the northern end of South Island. The uniform gravity trend on the southeast side of the Wairau Fault is a reflection of deep-seated variations in the thickness or composition of Alpine greywacke. Northwest of the Wairau Fault, the Brook Street high and the ultramafic high are superimposed upon the uniform trend. The anomalies are due to the fact that the rocks representing the Brook Street volcanics and the Wairau ultramafic mass are denser than the average basement rock.

2. THE REGIONAL BOUGUER ANOMALIES: These were used to remove the regional field from the Bouguer field and were plotted from values of gravity stations located on basement rock with a density of 2.67–2.7 gm/cc for the northern part of South Island (Fig. 3).

3. THE RESIDUAL ANOMALIES: Local grav-
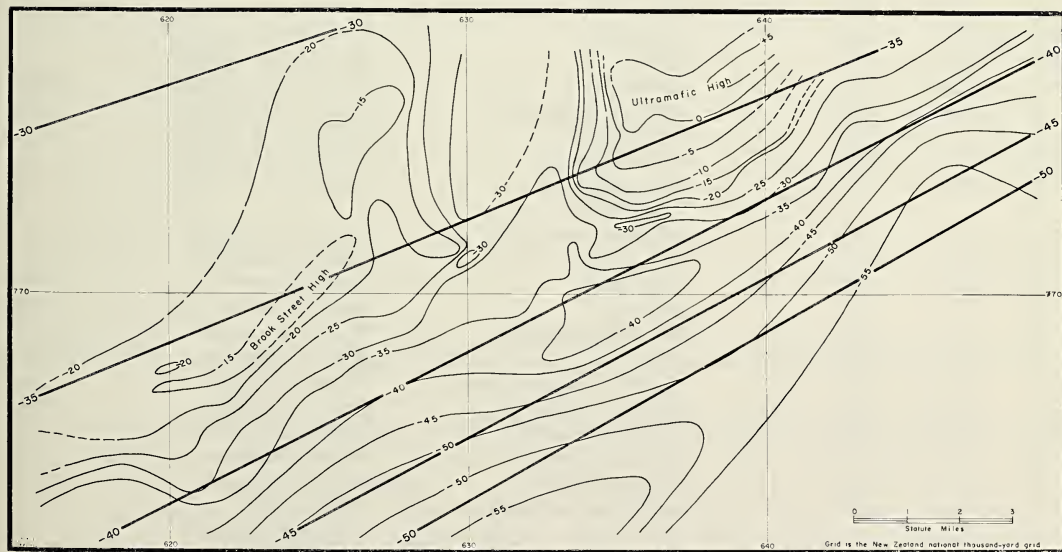
FIG. 3. Bouguer gravity anomaly pattern for the Tophouse district. Bold lines indicate regional Bouguer gravity trend. Contour interval at 5 mgal.

TABLE 5

DENSITIES AND MAGNETIC SUSCEPTIBILITIES OF REPRESENTATIVE ROCKS OF THE TOPHOUSE DISTRICT

DRY	WET	PART.	*	ROCK TYPE	FORMATION	MAGNETIC SUSCEPT., CGS UNIT $\times 10^{-6}$
3.30	3.30	3.30	0	dunite	Wairau ultramafic mass	
3.30	3.30	3.30	0	dunite	Wairau ultramafic mass	
2.93	3.02	3.21	9	weathered dunite	Wairau ultramafic mass	
3.19	3.19	3.19	0	pyroxene peridotite	Wairau ultramafic mass	206
3.20	3.20	3.21	0	pyroxene peridotite	Wairau ultramafic mass	247
3.33	3.33	3.34	0	dunite	Wairau ultramafic mass	
3.34	3.34	3.35	0	dunite	Wairau ultramafic mass	
3.32	3.32	3.32	0	harzburgite	Wairau ultramafic mass	204
3.11	3.13	3.18	2	harzburgite	Wairau ultramafic mass	
3.24	3.25	3.27	1	weathered dunite	Wairau ultramafic mass	
3.26	3.27	3.30	1	pyroxene peridotite	Wairau ultramafic mass	220
3.24	3.24	3.25	0	pyroxene peridotite	Wairau ultramafic mass	
2.68	2.68	2.68	0	hard serpentinite	Wairau ultramafic mass	
2.83	2.84	2.84	1	hard serpentinite	Wairau ultramafic mass	2840
2.56	2.58	2.61	2	hard serpentinite	Wairau ultramafic mass	1960
2.66	2.66	2.67	0	hard serpentinite	Wairau ultramafic mass	1300
2.92	2.94	2.97	2	serpentinized dunite	Wairau ultramafic mass	
2.57	2.60	2.66	3	soft serpentinite	Wairau ultramafic mass	940
2.22	2.34	2.53	12	soft serpentinite	Wairau ultramafic mass	1435
2.88	2.88	2.89	0	amphibolite	Wairau ultramafic mass	
2.88	2.89	2.91	1	amphibolite	Wairau ultramafic mass	
2.91	2.92	2.93	1	amphibolite	Wairau ultramafic mass	
2.87	2.89	2.92	2	amphibolite	Wairau ultramafic mass	430
2.92	2.93	2.95	1	red volcanic breccia	Wairau ultramafic mass	
2.81	2.84	2.90	3	spilite		
2.86	2.87	2.91	1	spilite		125
2.93	2.94	2.95	1	dolerite		66
2.79	2.80	2.82	1	red and green schist		120
2.76	2.78	2.80	2	green schist		
2.99	2.99	3.00	0	spilite	Brook Street volcanics	
2.89	2.90	2.92	1	spilite	Brook Street volcanics	
2.90	2.90	2.91	0	spilite	Brook Street volcanics	1000
2.78	2.80	2.84	2	volcanic agglomerate	Brook Street volcanics	93
2.61	2.64	2.69	3	volcanic tuff	Brook Street volcanics	38
2.68	2.69	2.70	1	hard limestone	Rangitoto formation	0
2.67	2.68	2.69	1	grey calcareous sandstone	Rangitoto formation	0
2.60	2.63	2.67	3	calcareous sandstone	Rangitoto formation	0
2.64	2.67	2.71	3	grey slate	Greville formation	22
2.63	2.68	2.75	5	grey slate	Greville formation	20
2.68	2.71	2.77	3	grey slate	Greville formation	20
2.74	2.77	2.82	3	red and green slate	Waiua formation	
2.34	2.47	2.69	13	tuff	Waiua formation	40
2.71	2.73	2.75	2	metasomatized volcanics	Waiua formation	58
2.82	2.85	2.90	3	volcanic sandstone	Stevens formation	230
2.92	2.95	2.94	1	volcanic sandstone	Stevens formation	50
2.70	2.72	2.77	2	volcanic siltstone	Stevens formation	
2.67	2.71	2.79	4	volcanic siltstone	Stevens formation	50
2.61	2.63	2.66	2	greywacke sandstone	Alpine facies (Raglan series)?	
2.62	2.62	2.64	0	greywacke sandstone	Alpine facies (Raglan series)?	

TABLE 5 (continued)

| DENSITY | | | | ROCK | | MAGNETIC SUSCEPT., CGS UNIT |
DRY	WET	PART.	*	TYPE	FORMATION	$\times 10^{-6}$
2.44	2.51	2.62	7	greywacke sandstone	Alpine facies (Raglan series)?	34
2.61	2.63	2.66	2	greywacke sandstone	Alpine facies (Raglan series)?	
2.67	2.69	2.72	2	haematitic chert	Alpine facies (Raglan series)?	39
2.67	2.68	2.69	1	greywacke sandstone	Alpine facies **	
2.66	2.67	2.67	1	greywacke sandstone	Alpine facies **	30
2.63	2.65	2.67	2	greywacke sandstone	Alpine facies **	120
2.74	2.75	2.76	1	argillite	Alpine facies **	74
2.75	2.76	2.79	1	argillite	Alpine facies **	
2.74	2.75	2.77	1	argillite	Alpine facies **	
2.72	2.72	2.73	0	argillite	Alpine facies **	
2.66	2.68	2.70	2	greywacke conglomerate	Alpine facies **	40
2.67	2.68	2.69	1	greywacke sandstone	Alpine facies	49
2.64	2.65	2.67	1	greywacke sandstone	Alpine facies	28
2.82	2.85	2.90	3	calcareous spilite	Alpine facies	360

* Porosity (%).
** Alpine facies (Mt. Robert series).

TABLE 6

PREFERRED DENSITIES OF ROCKS USED IN GRAVITY REDUCTIONS OF THE TOPHOUSE DISTRICT

ROCK	DENSITY (GM/CC)	DENSITY CONTRAST WITH STANDARD ROCK (GM/CC)
Alpine greywacke	2.70	0.00
Pleistocene gravels	2.25	−0.45
Stevens form. siltstone	2.78	0.08
Stevens form. sandstone	2.92	0.22
Waiua form. banded slate	2.82	0.12
Greville form. argillite	2.74	0.04
Rangitoto form. limestone	2.70	0.00
Te Anau ser. dolerite	2.95	0.25
Te Anau ser. spilite	2.90	0.20
Te Anau ser. red and green volcanic breccia	2.95	0.25
Serpentinite	2.65	−0.05
Dunite, pyroxenite	3.30	0.50
Brook Street volcanics (spilite)	2.94	0.24

ity anomalies show up more clearly in the residual gravity map (Fig. 4) and are quantitatively related to the surface geology.

The axis of the Brook Street high extends 1 mile west of Tophouse and gravity values decrease in that direction. Anomaly contours below the value of + 16 mgal appear to extend in a southwest direction from Lake Rotoiti. The axis of the Brook Street high has a north-to-south trend above Tophouse. This direction is parallel to the strike of the Brook Street volcanics, the Maitai series, and the strike of the Waimea Fault. The maximum positive value of 22 mgal is considered to indicate the position
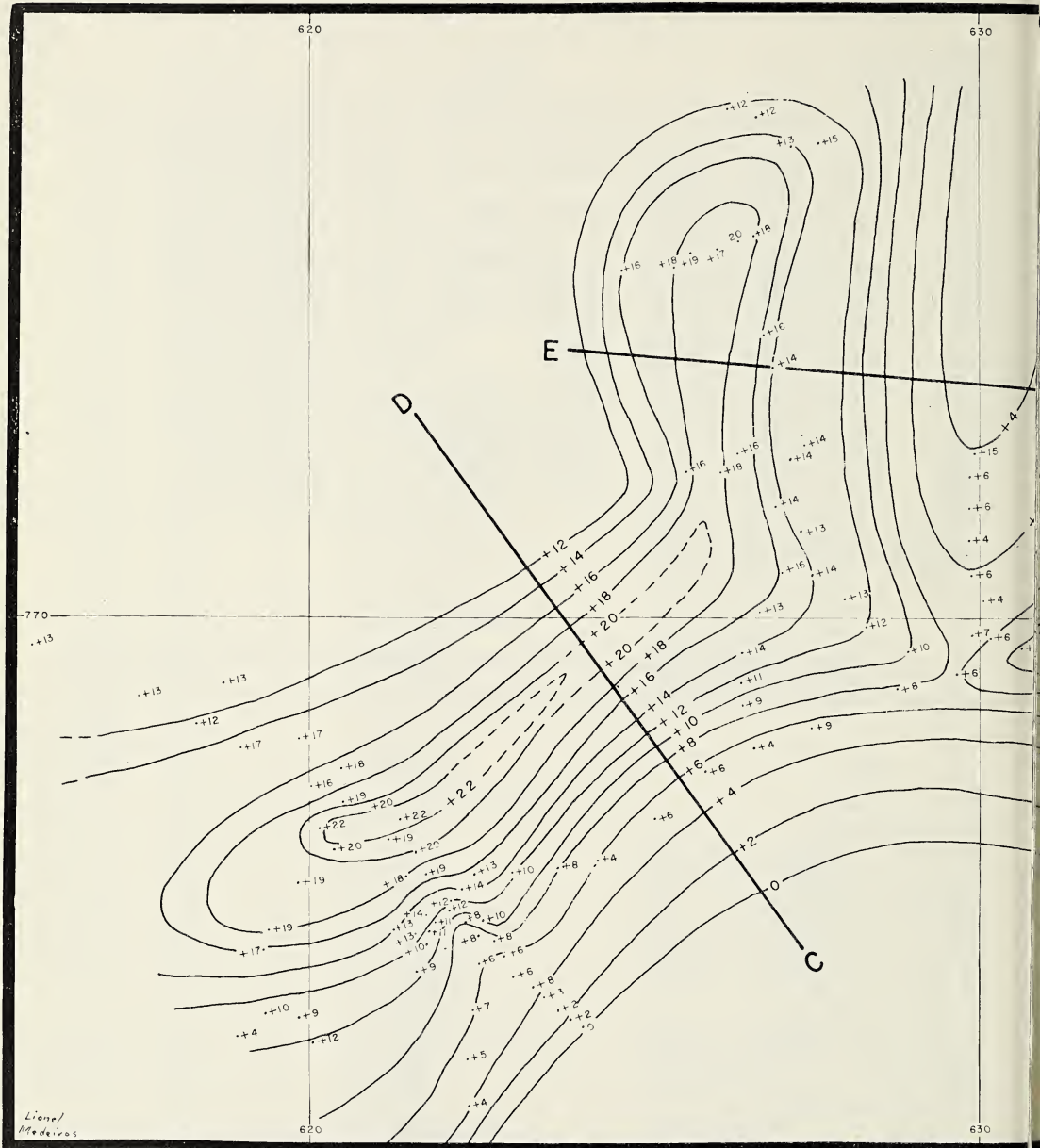
FIG. 4. Residual gravity anomaly pattern for the Tophouse district. Contour interval at 2 mgal. Lines A–B, C–D, and E–F show location of gravity profiles (see Figs. 5, 6, and 7, respectively).

Grid is the N.Z. national one-thousand yard grid
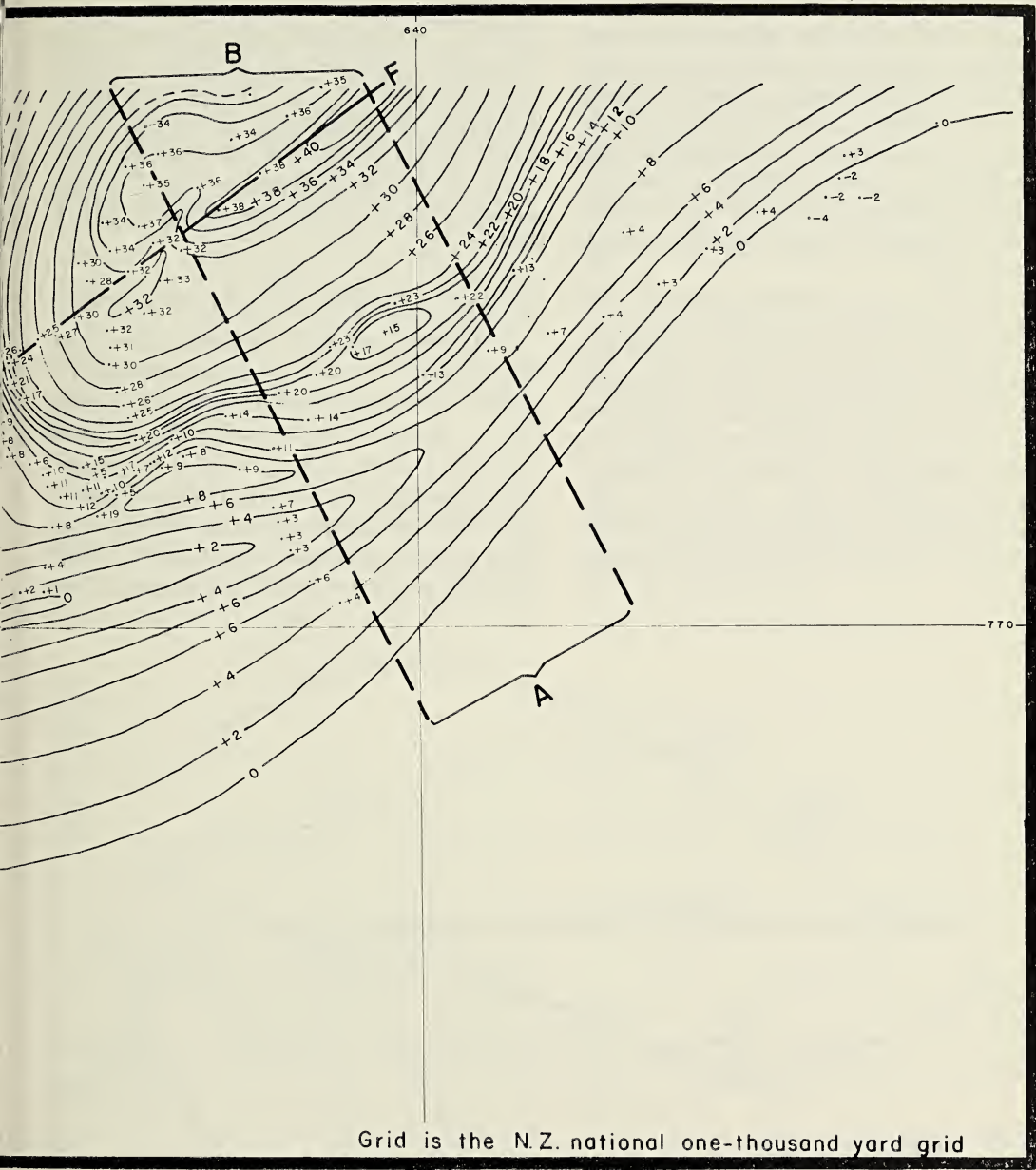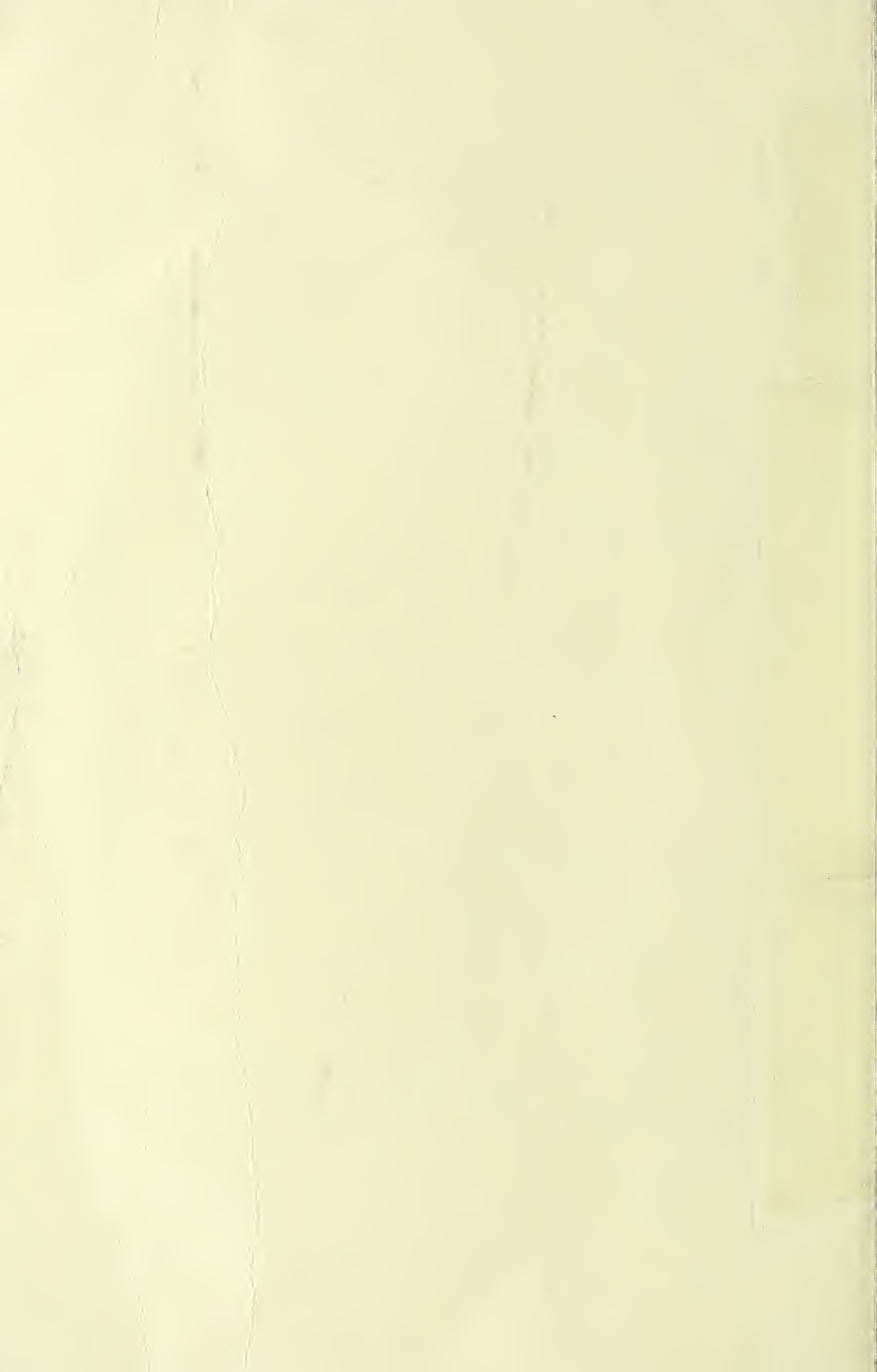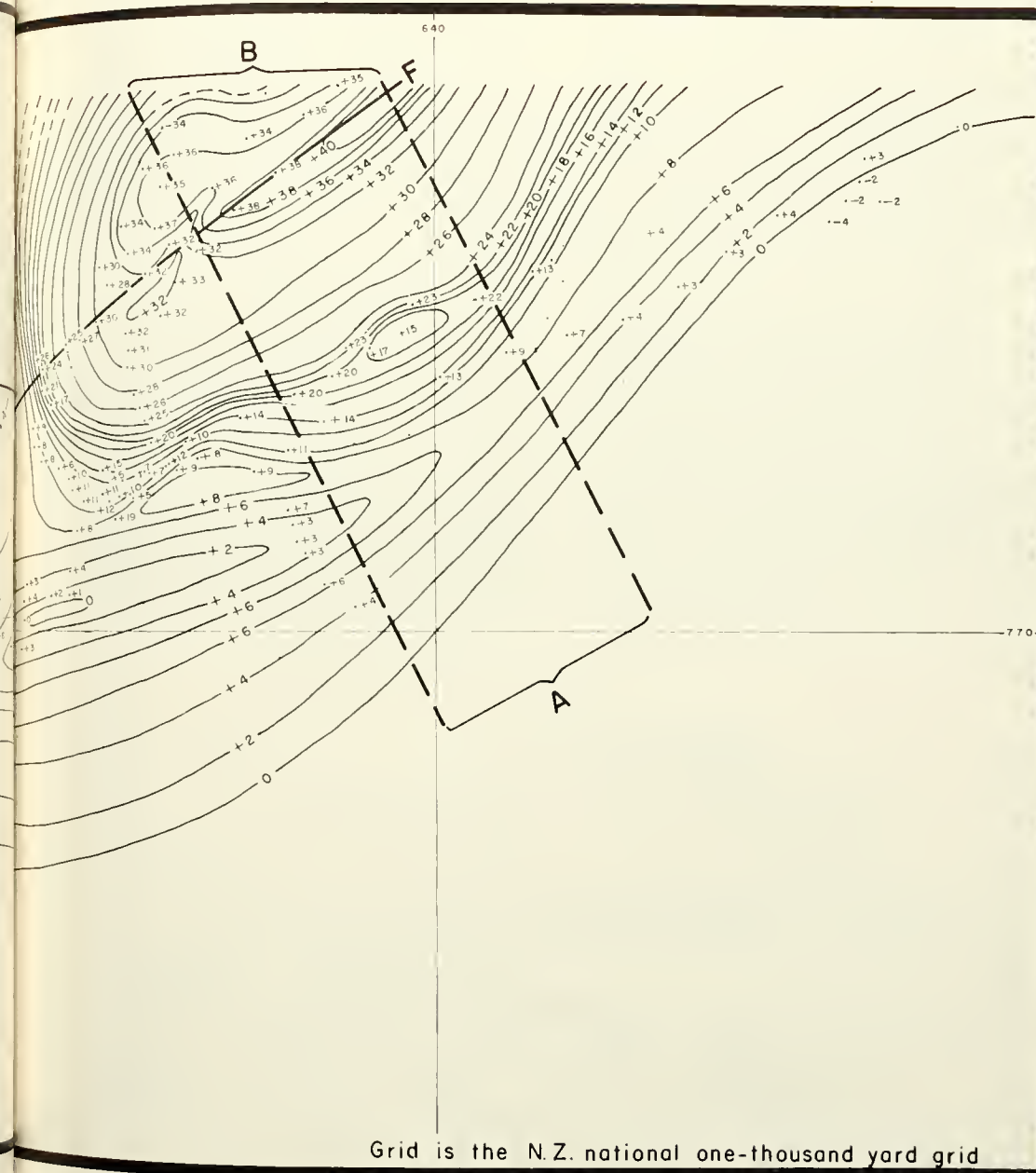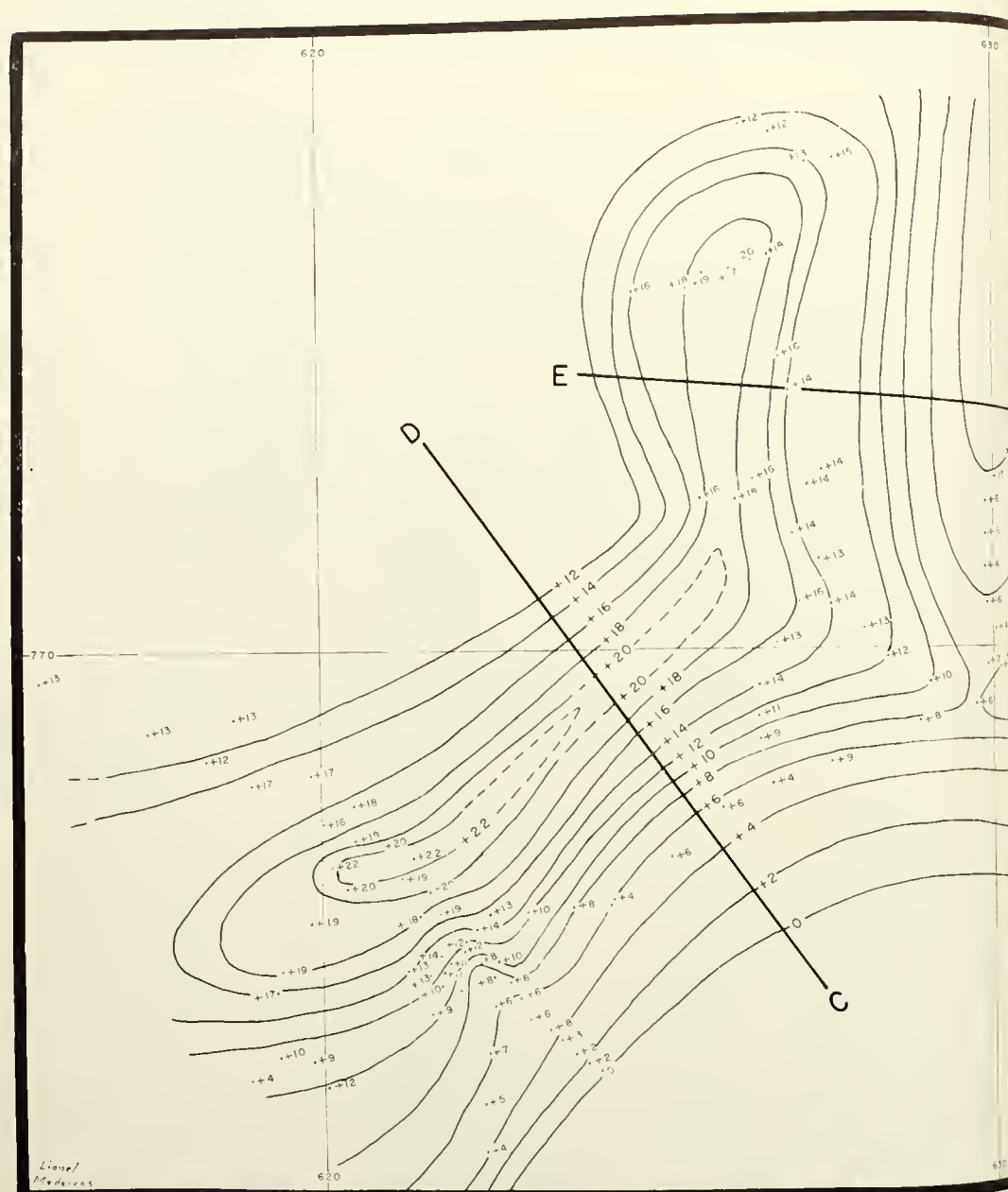
FIG. 4. Residual gravity anomaly pattern for the Tophouse district. Contour interval at 2 mgal. Lines A–B, C–D, and E–F show location of gravity profiles (see Figs. 5, 6, and 7, respectively).

of the maximum thickness of the volcanics below sea level. The Brook Street volcanics are flanked to the west by the Rotoroa igneous complex and to the east by the Maitai series. South of Tophouse Hotel, however, the axis of the Brook Street high swings around to strike parallel to the Wairau Fault. The change in the axial trend of the gravity anomaly from south to southwest is attributed to the bending and dragging of the Brook Street volcanics by transcurrent movement along the right lateral Wairau Fault.

The ultramafic high reaches a maximum positive value of 40 mgal. Along the margin, the gravity gradient is steep and it is inferred that the contacts surrounding the Red Hill ultramafic mass are also steep. Small gravity lows near the crest of the anomaly are attributed to shallow inclusions of serpentinite. The serpentinite along Maitland Fault is not reflected by a gravity low and is therefore considered to be underlain at a depth of a few hundred feet by peridotite.

The small negative anomaly of 4 mgal at the eastern bay of Lake Rotoiti is inferred to be caused by about 600 ft of glacial outwash gravel and silt. Another small negative anomaly with a maximum negative value of about 7 mgal is situated along the Wairau Valley 1 mile east of the Tophouse saddle and is inferred to be caused by about 1,000 ft of alluvium. No negative anomalies were observed over the Tophouse saddle, where the alluvium is about 300 ft thick.

Structure of the Maitai and Te Anau Rocks

1. GRAVITY ANOMALY PROFILES: Two regular geological features are represented by the gravity contours. One is the contact between the Rotoroa igneous complex and the Brook Street volcanics at depth, and the other is the contact between the peridotite of the Wairau ultramafic mass and Alpine greywacke at the Wairau Fault. These two structures have been studied in detail. The three gravity profiles are drawn perpendicu-
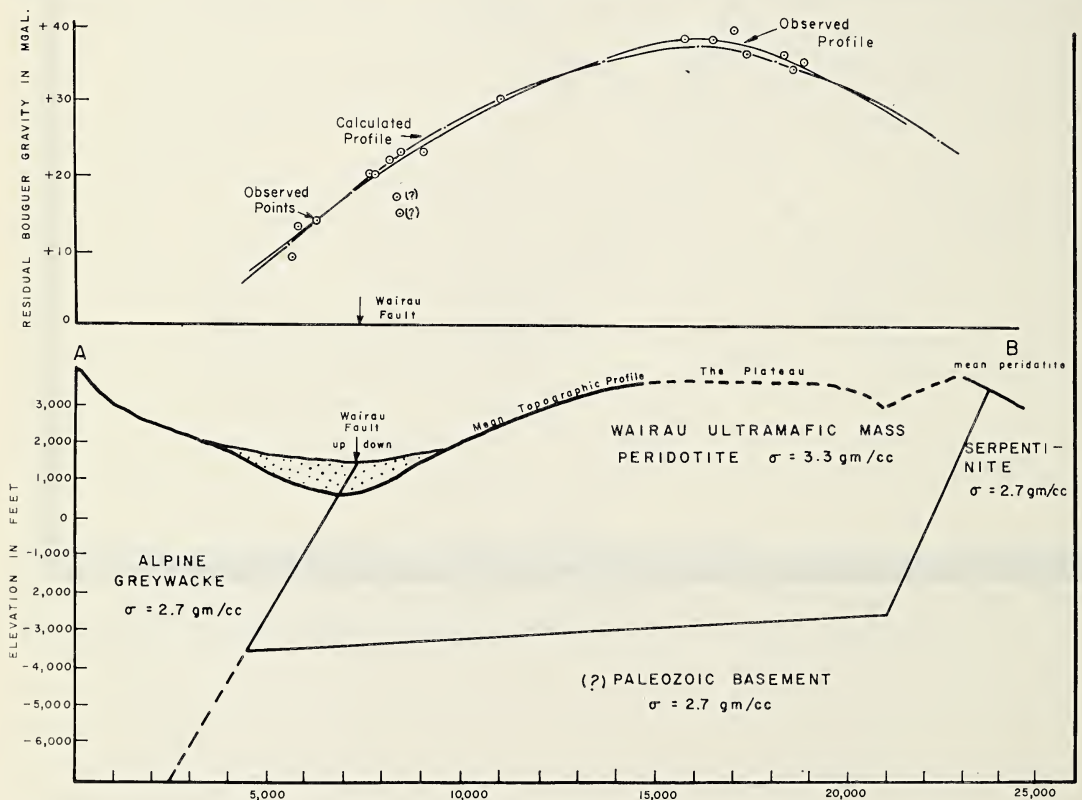
FIG. 5.   Gravity profile A–B across the Wairau ultramafic mass.

lar to the residual gravity anomaly contours and are shown in Figure 4.

Profile A–B (*Fig. 5*): *Alpine Greywacke–Wairau Fault–Wairau Ultramafic Mass.* In order to eliminate local irregularities, the average gravity values over a 2-mile-wide belt were taken normal to the anomaly contours as shown by profile A–B. Two of the observed values, marked by question marks in Figure 5, fall well below the others and have been neglected. A model with a theoretical curve which fits the observed curve to within 0.1 mgal is shaded. This model represents a simplified geological cross section across the Wairau ultramafic mass. A northeast dip of 67° for the Wairau Fault provides the best gravimetric solution and is probably correct to within 15°.

Profile C–D (*Fig. 6*): *Brook Street Volcanics –Waimea Fault–Wairau Fault.* Gravel and moraine obscure the contact between the Brook Street volcanics and the Rotoroa igneous complex. The western contact of the volcanics is at the Waimea Fault and gravimetric studies

show that the axis of maximum thickness of the volcanics lies 3 miles west of the fault outcrop.

The calculated gravity profile for the geological model (shaded) fits the observed curve to within 0.5 mgal along the margins of the curve. The peak of the calculated profile falls below the peak of the observed profile by 3 mgal. The differences can be resolved only by assuming that the density of the Brook Street volcanics is not uniform throughout and it is likely that denser rocks underlie the surface rocks.

Profile E–F (*Fig. 7*): *Rotoroa Igneous Complex–Brook Street Volcanics–Maitai Series–Wairau Ultramafic Mass.* The profile is perpendicular to the regional strike of the rocks and extends east from the Brook Street volcanics to the Maitai series and then northeast to the Wairau ultramafic mass. Observed values are irregular over the Wairau ultramafic mass and values have been averaged over a width of 2 miles along the profile.

The calculated gravity curve for the assumed
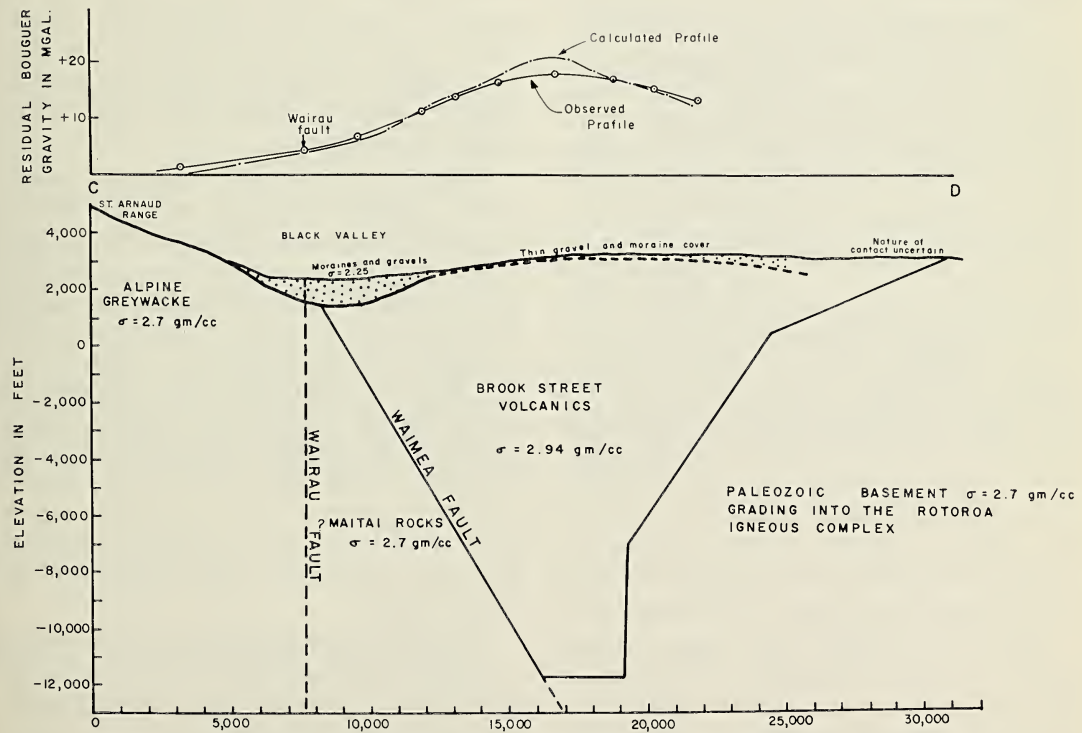
Fig. 6. Gravity profile C–D across the Wairau Fault, near Tophouse district.
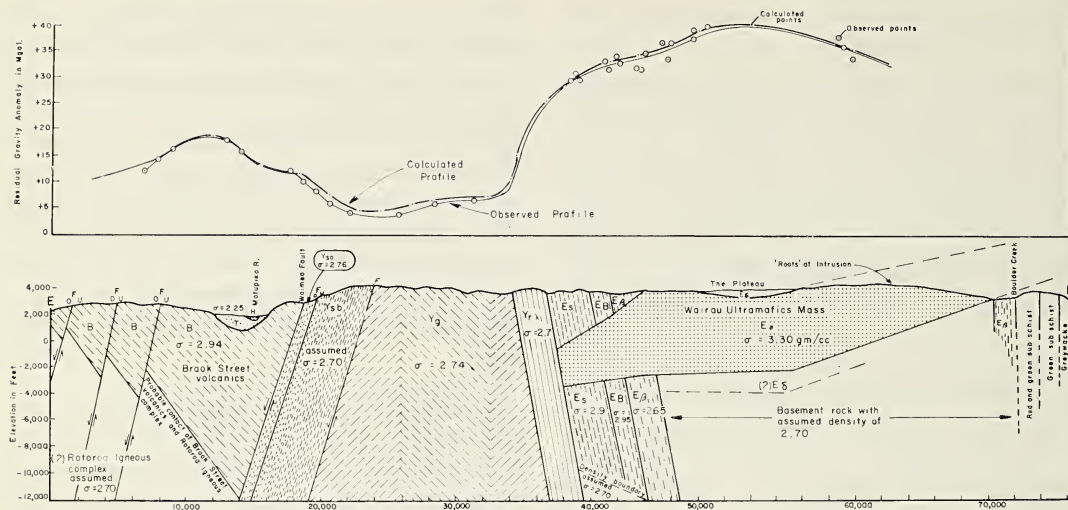
FIG. 7.   Gravity profile E–F across the Brook Street volcanics to the Wairau ultramafic mass.

densities fits the observed curve to within 2 mgal in all places. The most surprising feature of the profile is the 90° angle between the dips of the Maitai series–Te Anau volcanics and the attitude of the calculated base of the Wairau ultramafic mass.

2. DISCUSSION OF GEOLOGICAL STRUCTURE AS INTERPRETED FROM GRAVITY RESULTS: The Brook Street volcanics lie between the Waimea Fault to the east and the Rotoroa igneous complex to the west. The Waimea Fault has been observed to dip steeply west and the Brook Street volcanics have been observed to dip between 50° and 60° east. Interpretation of the gravity profiles shows that the Waimea Fault dips 70° west and that the maximum stratigraphic thickness of the Brook Street volcanics in the Tophouse district is about 13,000 ft, reaching a maximum vertical thickness of 12,-000 ft near the Waimea Fault. The Brook Street volcanics are probably underlain by rocks of the Rotoroa igneous complex, for which a density of 2.7 gm/cc has been assumed. The nature of this contact is unknown. A series of faults west of the Waimea Fault have been observed from air photographs and appear to dip steeply west.

Rocks of the Maitai series range in density from 2.70 gm/cc (Rangitoto formation) to 2.92 gm/cc (Stevens formation sandstone). However, no significant gravity anomalies were observed over these rocks, and it is inferred

that the denser rock members do not extend to depth as expected from surface observations and are probably underlain by Maitai rocks with a mean density of 2.7 gm/cc at depth.

Te Anau spilite, dolerite, and red and green volcanic breccia, with a mean density of 2.9 gm/cc, lie east of the Maitai series. Gravity results suggest that these relatively dense rocks are underlain at 12,000 ft below sea level by rocks of standard density. The nature of the contact is uncertain.

Geological interpretation of the positive gravity anomaly associated with the Wairau ultramafic mass has been based on two profiles (Figs. 5 and 7) constructed from average values over a width of 2 miles. Gravity values indicate that the peridotite is about 7,000 ft thick, with a maximum thickness below the Plateau (Fig. 7). South of the Plateau, the peridotite is faulted by the Wairau Fault against Alpine greywacke. At the fault contact the average dip from the surface down to the base of the peridotite appears to be 67° southeast with an error of about ± 15°. The Wairau ultramafic mass does not extend southward beyond the Wairau Fault.

A subsurface western extension of the Wairau ultramafic mass below the Te Anau volcanics is necessary in order to explain the large positive gravity values observed over the volcanics. The peridotite apparently intrudes the upper

Te Anau volcanics, probably up to the base of the Maitai limestone. The peridotite, therefore, is younger than the volcanics and older than the Rangitoto (Maitai) limestone. The present shape of the ultramafic mass is that of a horizontal sheet with near-horizontal structures such as low-angle dipping bands. Hence, if the original dip of the Te Anau volcanics and the Maitai series was horizontal, the original dip of the Wairau ultramafic mass was probably vertical. This suggests a vertical mode of emplacement for the Wairu ultramafic mass. The inferred relationship (Grindley, 1958: 35) can be seen by turning Figure 7 sideways, so that the Maitai series are at the top. The peridotite of the ultramafic mass could have been intruded vertically after the extrusion of serpentinite lavas, the red and green volcanic breccia, and the spilite. After the intrusion of the peridotite, a period of erosion was followed by the deposition of the Rangitoto limestone and the rest of the Maitai series. Later, regional tilting and folding exposed the "roots" (Fig. 7) of the ultramafic mass. The roots were subsequently destroyed by erosion.

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NOTE

A Noninjurious Attack by a Small Shark[1]

David P. Fellows and A. Earl Murchison[2]

Aside from the general need for thorough documentation of shark incidents (Hobson, et al., 1961:605), the following shark attack is worthy of report for two reasons: (1) The shark was of small size. (2) Immediately prior to attack the shark displayed a behavior pattern which is mentioned only briefly in the literature.

Description of the Incident

The shark, a 3-ft *Carcharhinus menisorrah,* was encountered while the authors were baiting eel traps with freshly speared fish in a large pothole in the lagoon reef at Johnston Island. At the time (1400 hours, 19 December 1965), water temperature was 26° C and underwater visibility more than 100 ft. The weather was cloudy with intermittent rain, a strong wind was blowing, and the surface of the sea was choppy. Both divers were wearing dark trunks and black neoprene wetsuit jackets.

The attack occurred during an attempt to take the shark by spear for research purposes. Armed with a "Hawaiian sling," Fellows closed to within 7–8 ft of the shark and then began to follow the shark as it swam slowly in a path roughly describing a circle about 50 ft in diameter. During the first lap of the chase, the shark swam in an unexcited manner approximately 5 ft above the bottom of the pothole (which was about 15–25 ft deep). Immediately after beginning the second lap, the shark commenced a radically different swimming behavior; the tailbeat frequency decreased noticeably and the shark simultaneously began to swing the entire anterior portion of the body slowly from

side to side in a greatly exaggerated swimming motion. The headswinging was sufficient to bring the entire head profile into view by Fellows, who at this time was directly behind and about 5 ft away from the shark. This behavior was continued for slightly less than half a lap, at which time Fellows surfaced for air. When Fellows surfaced, the shark, swimming over a coral mound, rose to within approximately 6 ft of the surface, passed directly below Murchison, and descended back to within 5 ft of the bottom. As the shark approached Murchison during its ascent, the exaggerated swimming motion stopped. Immediately after passing under Murchison the shark began to swim more rapidly, resumed the exaggerated manner of swimming, and, when 25 ft away, turned and made a very rapid dash directed at Fellows's arm. During the approach the shark's mouth was open approximately 1 inch. Fellows twisted violently aside, and the shark missed his arm and passed between his legs. When five ft behind Fellows, the shark turned and made a second high-speed pass. On this pass the diver's swim fin made solid contact with the shark, but whether contact was due to Fellows's thrashing or to directed attack by the shark is uncertain. Either way, contact was sufficient to discourage the shark, which rapidly departed from the area. During the two passes the divers were about 7 ft apart.

Discussion

Although the total time of the encounter with the shark occupied less than 3 minutes, and the duration of the actual attack less than 10 seconds, both observers readily noted four items: (1) At the beginning of the chase the shark showed no overt response to the divers' presence. (2) The headswinging behavior began only after the pursuer got within what appeared

to be a critical distance. (3) Headswinging behavior immediately preceded attack behavior. (4) Headswinging behavior appeared only when the diver was behind the shark.

The same exaggerated swimming motion has been reported by Hobson (1961:29) as occurring in at least two species of *Carcharhinus*. In one case the behavior immediately prefaced an attack on a diver at Wake Island. The present authors agree with Hobson's opinion that the behavior permits the maintaining of visual contact with an object directly behind the shark, but they also suggest that the behavior might signal an intention of attack on the part of a harassed shark.

It is the opinion of the authors that the incident reported here was a defensive behavior by the shark, provoked by pursuit in a confined area.

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BATZO, RODERICK L., and J. K. RIPKIN. 1849. A Treatise on Pacific Gastropods. Rice and Shipley, Boston. vii + 326 pp., 8 figs., 1 map.

CRAWFORD, DAVID L. 1920a. New or interesting Psyllidae of the Pacific Coast (Homop.). Proc. Hawaii. Ent. Soc. 4(1):12–14.

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PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL AND PHYSICAL SCIENCES OF THE PACIFIC REGION

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PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL AND PHYSICAL SCIENCES OF THE PACIFIC REGION

CONTENTS

CONTENTS (*continued*)

Deep Cores of Oahu, Hawaii and Their Bearing on the Geologic History of the Central Pacific Basin

Harold T. Stearns and Theodore K. Chamberlain[1]

In the Central Pacific Basin few studies of the earth's crust have been made, and those studies that have been undertaken have been mainly geophysical in nature: seismic, magnetic, heat flow, and gravity surveys. These geophysical data usually require for their correct interpretation some knowledge of the geologic properties of the crust, especially the upper crust; consequently, in order to supplement these geophysical data and for other more direct reasons, e.g., stratigraphic, palaeontologic, petrologic, etc., there has been for a long time a desire to take actual samples of the Central Pacific Basin crust. To realize this goal H. S. Ladd, J. I. Tracey, K. O. Emery, and others in the last twenty years have drilled several deep holes on Central Pacific islands. Unfortunately, the drilling techniques used did not allow the recovery of a core sample, so that actual lithologic sections of the upper crust were not obtained.

In October 1964 a grant was obtained from the National Science Foundation by the authors to drill a series of deep holes on the edge of the Ewa Coastal Plain, Oahu, Hawaii. The intent of this research program was to obtain complete sections of the upper crust utilizing a newly developed core barrel that allows nearly 100% core recovery. The Ewa Coastal Plain was chosen as the drilling site because it is the widest coastal plain in the Central Pacific Basin, thereby allowing the drilling to be done farther from the central island core than elsewhere in the Pacific.

The results obtained by drilling the first two holes were very rewarding. The first hole (Ewa No. 1) was drilled on the 158th meridian 200 yards inland from the beach (Fig. 2, inset). The basaltic core of Oahu was penetrated beneath 1,072 ft of interbedded coral reefs,

lagoonal muds, sands, and soils. The second hole (Ewa No. 2) was drilled also on the 158th meridian about 2 miles inland from Ewa No. 1. In the second hole 517 ft of sedimentary rocks were penetrated before the basement basalts were encountered. More than 85% of the core was recovered in both holes, the first time in the Central Pacific Basin that such complete cores have been obtained from deep holes in the upper crust.

Not only are the recovered cores valuable in deducing the geologic history of the Central Pacific Basin but, because of their location on Oahu, they allow tectonic and eustatic deductions to be made concerning the submergence and emergence of the Hawaiian Archipelago. Furthermore, the Ewa holes are related to other deep drilling investigations in the Hawaiian area planned for the near future:

1. It is the desire of the authors to drill two more deep holes offshore along the 158th meridian to complete the stratigraphic section across the Ewa Coastal Plain. These offshore holes will be in water about 1,800 ft deep and will penetrate approximately 2,000 ft of crustal sediments.

2. Since the Oahu drilling was completed
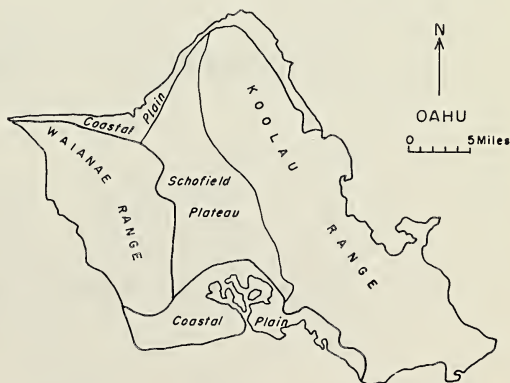
Fig. 1. Map of Oahu showing Ewa Coastal Plain on the south shore of the island.

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Fig. 2. North-south geologic section across Ewa Coastal Plain, Oahu.

two holes have been drilled into the basaltic basement of Midway Atoll. The same equipment used on the Oahu holes was used there. These holes penetrated deeply weathered basalt overlain by basaltic conglomerates, marine sediments, and coral reefs similar to those above the Oahu holes, indicating a long erosional and weathering period in the history of ancient Midway volcanoes prior to submergence (Stearns, 1966).

3. A proposal exists to drill a hole in the Kailua area of eastern Oahu to study the mantle-like material that appears to be close

to the surface in that area. The hole will be drilled on land and probably will be over 6,000 ft deep.

All of the above studies are related in that geologic data in the form of complete lithologic sections of the crust are to be obtained by deep drilling. These data will allow a more complete understanding of the geologic history of the Central Pacific Basin and a more exact knowledge of the tectonic and eustatic history of the Hawaiian Archipelago.

The two holes (Ewa Nos. 1 and 2) recently
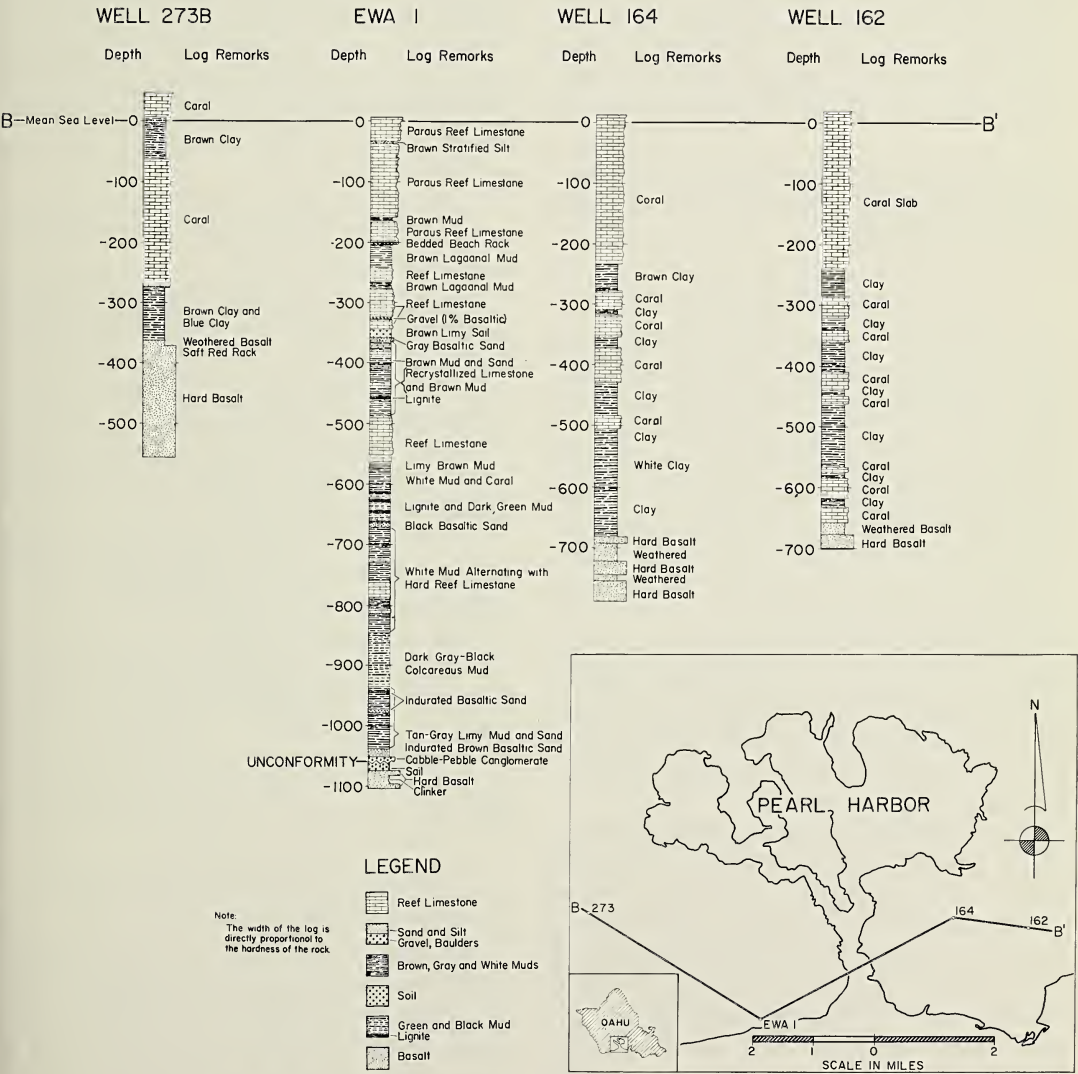
FIG. 3.   East–west geologic section across Ewa Coastal Plain, Oahu.

drilled on the Ewa Coastal Plain are not the only holes that have been drilled on that plain. Hundreds of wells have been drilled from Barber's Point to Honolulu and from the mountains to the sea during the past 40 years (Stearns and Vaksvik, 1935, 1938). However, no samples were saved from these holes. Logs of these wells are frequently ambiguous as to terminology; "coral" and "limestone" are used interchangeably, and it is suspected that any white rock penetrated by the drill was logged as "coral."

Using recovered cores from Ewa Nos. 1 and 2, however, it has been possible to go back to these earlier logs and reinterpret them. In this manner a great deal of additional information was obtained that could be used to extrapolate the data from the Ewa holes (Figs. 2 and 3).

Mr. William Ebersole assisted in the project The holes were drilled by Layne International Company of Honolulu.

LITHOLOGIC TYPES

The sedimentary rock in the two Ewa cores consists mainly of various types of reef limestone alternating with shallow-water muds. A few soils, a layer of beach rock, two beds of lignite, basaltic sands, and stream conglomerates were encountered. The igneous rock recovered in the lower portion of each core consists of alternate flows of pahoehoe and aa basalt. Lithologic terms used throughout the following discussion are defined below:

Reef limestone. A sedimentary rock consisting of the remains of various corals, mainly *Porites,* calcareous algae, molluscs, etc., essentially in position of growth. Much of the original skeletal material has been replaced by secondary calcite and/or dolomite.

Mud. A marine or fresh water sediment consisting of particle diameters mainly in the silt and clay size range, i.e., 1/16 mm to about 1/1000 mm, and composed of various detrital minerals resulting from terrestrial weathering. Marine shells may be present. The various types of muds are described in terms of their colors; the muds in the Ewa cores owe their colors to the following constituents: (a) oxides of iron and aluminum (brown mud); (b) iron

sulfides and organic detritus (black mud); (c) calcium carbonate particles mixed with brown or black mud (gray mud); (d) clay size particles of calcium carbonate presumably reef detritus (white mud); (e) clay minerals and ferrous iron (green mud).

Beach rock. A sedimentary rock consisting of calcareous beach sand cemented by calcium carbonate. Beach rock is commonly found forming within the beaches of tropical islands and owes its origin to the seepage of carbonate-rich ground waters through a beach composed of calcium carbonate particles. Beach rock is formed only at or within the tidal range and positively indicates a former shore line.

Reef breccia. A sedimentary rock composed of the angular fragments of an organic reef. The broken fragments may be $1/2$–4 inches in diameter and are commonly mixed with sand and silt-size reef debris.

Lignite. Fossil plant remains altered by pressure to a highly friable, soft, black sedimentary rock. A low grade of coal.

Conglomerate. A sedimentary rock composed of rounded cobbles and pebbles intermixed with finer material.

Clinker. Rough, spinose, vesicular fragments of lava produced by lava flow.

Pahoehoe basalt. Lava with a smooth or ropy surface spread chiefly through tubes and characterized by round vesicles.

Aa basalt. A lava flow with a rough clinkery surface and base. Deflated and stretched vesicles characterize the solid part of the flow.

Marl. A calcareous clay.

Soil. The term is used in a general way to mean regolith on the basalt and any sediment altered by weathering.

Cobbles, pebbles, gravel, sand, silt, clay. The usage herein follows the usual dictionary definitions.

MEGASCOPIC DESCRIPTION OF CORES

Ewa No. 1 (Table 1)

The drilling site for this hole was located as far seaward on the Ewa Coastal Plain as it was feasible to drill, within 200 yards of the sea on the 158th meridian on the eastern end of the property of the U. S. Coast and Geodetic Station, 91-270 Fort Weaver Road, Ewa Beach,

Oahu, opposite Ewa Beach Park. The terrace at this locality was a flat, low, emerged coral reef of undetermined age, partially covered with a thin discontinuous soil layer. The ground level is + 6.1 ft above mean sea level; all depths in the core are measured from ground level equaling zero.

Ewa No. 2 (Table 2)

The second hole on the Ewa Coastal Plain was also located on the 158th meridian but 2 miles inland from Ewa No. 1. The exact locality was within the confines of the West Loch of Pearl Harbor Naval Base, at a point a few hundred yards south of the West Loch shoreline. The ground level at the hole is 19.7 ft above mean sea level; all depths in the core are measured from ground level equaling zero.

PRELIMINARY SEISMIC DATA

On July 13 and 14, 1965 seismic refraction studies were made of the ocean bottom to the south of drilling site Ewa No. 1. The following results were obtained at a distance of 8.4 km seaward from the coast along the 158th meridian (21°15′N, 158°00′W): (1) water depth —0.36 km; (2) depth from sea surface to the upper surface of the basalt basement—1.1 km; (3) sound velocity in the sedimentary section = 2.8 km/second.

These data show the sedimentary column to be 2,920 ft in thickness at a distance of 4.6 miles offshore from Ewa No. 1 in a water depth of 1,182 ft. The sediment-basalt interface was found to be essentially parallel to the sea water-sediment interface.

PRELIMINARY GEOLOGIC HISTORY OF THE EWA COASTAL PLAIN

The following description applies to the outer edge of the Ewa Plain in the vicinity of Ewa No. 1:

1. Prolonged weathering and erosion of the upper surface of the Koolau basalts. Formation of thick soil deposits, deep incision of stream valleys, and deposition of stream cobbles, pebbles, and basaltic sand along the coast.

2. Gradual submergence.

3. Accumulation of thick deposits of shallow marine lagoonal sediments behind a barrier reef. Stream-transported muds and silts predominate, with occasional layers of basaltic sand and gravel. Inorganically precipitated $CaCO_3$ common to these sediments indicates a restricted oceanic circulation. Much of the mud is high in organic carbon, indicating swamp conditions. Typical lagoonal-deltaic sedimentary facies.

4. With continued submergence, the water deepened sufficiently to allow the lagoonal deposits to be superseded by calcareous muds and coral debris. These sediments indicate the barrier reef structure was in close proximity. The upper portion of this section grades into a hard reef limestone horizon at —786 ft MSL in the core.

5. Following the growth of these corals the progradation of the land was sufficient to shift the coral reef facies seaward, allowing at first the accumulation of gray calcareous mud and coral debris, and finally, the progradation of the land was sufficient to bring basaltic river sands and silts and dark-gray to black organic muds into the area. The environment again became swampy-lagoonal and eventually peat deposits accumulated, now represented by the lignite and soils found at —624 ft MSL. At this depth a major unconformity occurs which probably marks the Pleistocene-Pliocene boundary.

6. Following the deposition of the lignite beds the sea level rose, allowing the coral facies to shift landward. At first calcareous muds containing coral debris accumulated, but these were followed by the growth of marine coralline reefs more than 50 ft in thickness.

7. On top of this reef is found at first calcareous mud followed by brown mud and sands and soils, indicating a progradation of the lagoonal facies. At —406 ft MSL a minor unconformity occurs and continues upward through brown muds and basaltic sands and soils to a major unconformity at —358 ft MSL that most likely corresponds to the Kahipa-Mamala submarine shelf around Oahu (Stearns, 1966).

8. Subsequent to the development of this

TABLE 1

DESCRIPTION OF CORE FROM EWA NO. 1 HOLE

DEPTH (IN FEET)	ROCK TYPE	DESCRIPTIVE NOTES
0–2	Loose coral and sand	Hole started in exposed emerged coral reef.
2–41.8	Reef limestone	Coral in upright position of growth and reef debris.
41.8–43.8	Tuff (?)	Stratified fine grained material with thin horizontal calcite layers, possibly an altered tuff.
43.8–165	Reef limestone	Mostly *Porites* coral and nullipores. The corals are in upright position of growth. Starting at 96 ft the cavities in the reef limestone contain coatings of a red clay which X-ray and mineral analysis indicate is sediment derived from a basaltic terrane. The red mud becomes only a trace below 135 ft.
165–166	Brown mud with fragments of coral 1 inch across	
166–167	Brown compact mud	Brown mud full of fossil molluscs and fragments that represents a discontinuity.
167–203	Reef limestone	Hard white and cream colored reef with no soil in cavities.
203–209	Beach rock	Thin-bedded beach rock; contains about 10% basaltic grains, the rest Foraminifera, shell, and coral grains, very well rounded and cemented by calcite into hard limestone.
209–250	Brown mud	Brown mud containing 1–20% limestone grains.
250–270	Reef limestone	Hard fragmental reef with some brown mud in cavities. Much of it is recrystallized limestone.
270–283	Brown mud	Dark-brown organic mud mixed with coral fragments mostly 1 to 2 inches across.
283–290	Altered reef limestone	Soft, slightly muddy, powdery limestone; apparently altered top of reef containing thin limonite streaks.
290–311	Reef limestone	Fragmented limestone, mostly recrystallized and broken by drilling. Some heads of *Porites* and a few molluscs.
311–314	Muddy limestone	Recrystallized reef with 50% brown mud in interstices, mud content increasing downward.
314–315	Brown mud	About 90% brown mud and 10% limestone fragments.
315–331	Reef limestone	Muddy reef limestone, partly recrystallized.
331–333	Gravel (?)	Partly rounded reef limestone ½–1 inch across, mixed with similar size and shape basalt pebbles. Basaltic pebbles constitute 1% of deposit.
333–337	Reef limestone	Similar to 315–331 ft, with a few subrounded pebbles of basalt.
337–348	Reef limestone	Mud becomes whiter progressively with depth and decreases in quantity at 341 ft, where fragments increase in size.
348–350	Reef limestone	Same as above but white. Possibly the white mud is due to grinding action of bit.
350–355	Reef limestone	Brown mud filling interstices in a reef. Bit breaks it all up and makes a fragmental deposit with brown coating. Similar to 315–331 ft.
355–358	Limey mud breccia	White and brown mud with mostly small limestone fragments less than 1 inch across, a few 1½ inches across.

TABLE 1 (*Continued*)

Description of Core from Ewa No. 1 Hole

DEPTH (IN FEET)	ROCK TYPE	DESCRIPTIVE NOTES
358–363	Brown mud	Pure dark-brown mud with irregular tubular cavities ½ mm across lined with limonite. No bedding visible. Last 6 inches is light brown.
363–364	Gray sand	Gray-brown fine sand; over 50% basaltic grains eroded from a basaltic terrane or water-laid lithic tuff deposit. No glass particles obvious.
364–371	Calcareous mud	Calcareous mud with limonitic streaks.
371–376	Reef limestone	Muddy fragmental reef limestone, much altered.
376–383	Calcareous mud	White calcareous mud.
383–394	Reef limestone	Muddy fragmental reef limestone probably broken by bit.
394–401	Mud and coral fragments	Layers of mud and mixed mud and coral fragments.
401–412	Brown mud	Brown mud with scarce limy grains. A 4-inch layer of fine weathered basaltic sand from 403.5 to 404 ft.
412–415	Reef limestone	Muddy reef limestone, with about 1 ft of altered limestone at top with laminations.
415–435	White limy mud	White chalky mud with a few hard chunks. Contains minute borings of marine organisms. Probably a chemical precipitate. Lumps of hard limestone at 424 ft and from 426–435 ft. Some are altered coral fragments.
435–444	Reef limestone	Recrystallized reef limestone and white mud. Transition into material above. Mostly fragments broken up by drilling(?). At 440 ft mud becomes browner and at 444 ft becomes predominant over coral.
444–453	Brown mud and limestone fragments	Mud and coral reef limestone fragments.
453–464	Gray mud	Same as above but fewer rock fragments. Possibility that some rock fragments are chiefly crystallized calcite in place.
464–464.5	Organic mud	Brown layer with 1-inch layer of black lignite at bottom.
464.5–472	Gray mud	Gray lagoonal mud; in places 4 inches of it is hard cemented mud-limestone. Contains one oyster shell and a few other types of molluscs.
472–493	White mud	White calcareous mud with hard crystalline calcite lumps toward the bottom. Spherical and oval grains suggest altered Foraminifera.
493–497	Reef breccia (?)	Fragmental limestone containing large oyster shells and other molluscs. The mud matrix is darker than above. The whole deposit resembles a fine-grained reef talus deposit.
497–572	Reef limestone	Fragments of reef limestone ¼–3 inches across, probably broken by bit; probably highly permeable structure. Oyster shell at 523 ft. Mostly recrystallized. At 535–540 ft several zones of smaller sized fragments and white mud. Oyster at 546 ft. *Porites* at 545 ft. At 545–555 ft much recognizable coral, less altered than above.

TABLE 1   (*Continued*)

DESCRIPTION OF CORE FROM EWA NO. 1 HOLE

DEPTH (IN FEET)	ROCK TYPE	DESCRIPTIVE NOTES
572–575	Brown mud and lime	A brown mud full of streaks and nodules of lime and a few shells. At 575 ft a hard 1-inch layer of dark greenish claystone full of shells in excellent state of preservation.
575–585	White mud and lime	White calcareous mud full of nodules becoming indurated at 579–580 ft, then calcareous mud again.
585–590	Reef limestone	Highly altered fragmental reef.
590–597	White limy mud	White calcareous mud with nodules scattered throughout.
597–609	Greenish mud	Greenish calcareous mud, highly fossiliferous, containing irregular red iron oxide streaks.
609–617	White mud	At 611 ft in the white mud is a 1-inch layer of fine grained tuff. A few chunks of very hard chemically precipitated limestone.
617–629	Green and black mud	Greenish calcareous mud, highly fossiliferous to 623 ft, then organic mud becoming blacker with depth.
629–631	Lignite	Firm lignite full of fossil plant remains; no shells.
631–635	Gray-green mud	Calcareous organic mud full of shells.
635–646	Gray mud	Gray mud with shells.
646–660	Dark-gray mud	Mud is becoming more organic; still highly fossiliferous.
660–668	Green and black mud	Greenish-brown to olive black mud. Recognizable weathered basaltic grains. Few fossils.
668–675.8	Black sand	Thin-bedded, compact, fine basaltic sand and silt.
675.8–676.5	Fine sand	Fine calcareous sand and silt, highly fossiliferous.
676.5–686	Gray mud	Gray calcareous mud with two beds of black mud at 678 and 678.5 ft. Shells are in thin zones.
686–706	Tan mud	Tan mud full of fossils. A layer of calcareous sand with abundant rounded grains of basalt and one unweathered feldspar crystal possibly indicating tuff source at 692–693 ft. Laminated at 699 ft.
706–727	White mud	Chalky white mud; fossils scarce.
727–727.4	Brown mud	Firm brown mud.
727.4–728	Gray mud	Calcareous gray mud.
728–735.5	Reef limestone	Hard reef limestone; some layers contain grains of lime.
735.5–764	White mud and limestone nodules	Hard limestone fragments in white mud, possibly a breccia transitional to reef below.
764–792	Reef limestone	Highly altered fragmental reef limestone with a few shell molds and pockets of clay. White mud layer at 776–778 ft.
792–811	Gray mud	Gray calcareous mud, some limy streaks, and scarce solid nodules and concretions.
811–816	Reef limestone	Reef limestone.
816–851	Gray mud	Gray calcareous mud with hard nodules and concretions up to ⅜ inch across. Some indurated layers. At 846–851 ft some mixed gray and green mud.

TABLE 1 (*Continued*)

Description of Core from Ewa No. 1 Hole

DEPTH (IN FEET)	ROCK TYPE	DESCRIPTIVE NOTES
851–858	Olive black mud	Highly fossiliferous mud with sharp basal contact.
858–931	Gray and black mud	Gray calcareous mud with no nodules and some shells. At 874 ft a ½-inch layer of basaltic sand with some layers of gray-black and black mud, highly fossiliferous and full of basaltic grains and microscopic fossils. Some silt layers at 911–921 ft.
931–942	Olive black mud	Similar to above, poor in fossils, but uniformly dark.
942–948	Gray mud	Similar to above except for color.
948–950	Basaltic sand	Indurated basaltic sand and clay; basalt grains diverse and weathered.
950–966	Gray mud	Indurated gray calcareous mud. No fossils observed.
966–979	Brown mud	Indurated brownish-black mud.
979–930.5	Brown sand	Indurated fine basaltic sand and silt.
980.5–981.5	Brown clay	Indurated brown silty clay.
981.5–984	Brown sand and gravel	Indurated brown basaltic sand with scarce pebbles up to ½ inch across.
984–991	Brown mud	Indurated brown fossiliferous silty clay containing a 1-inch piece of *Porites* coral embedded in clay at 988 and 990 ft.
991–1015	Gray mud	Indurated gray mud with limy zones and nodules. Oyster at 1,004 ft and more at 1,009 ft. Another oyster at 1,015 ft.
1015–1043	Tan and gray mud	Hard very indurated brown mud, in places fossiliferous. Oyster shell, other fossils at 1,025 ft.
1043–1054	Brown sand	Typical brown basaltic indurated sand; grains mostly weathered limonite stained areas.
1054–1061.5	Conglomerate	Cobbles and pebbles up to 6 inches across, mostly dense blue basalt with a layer of silty clay, sand, and small pebbles at 1,055.5–1,057 ft. The sandy layers may be the matrix washed by drilling. Sand again at 1,061–1,061.5 ft.
1061.5–1072	Brown clay	Well indurated brown silty clay. No fossils noted. Basaltic grains visible. Becomes sandy at 1,071 ft for 1 ft.
1072–1077.5	Weathered basalt	Weathered basaltic aa clinker typical of a subsoil, consisting of partly decomposed clinker in a softer matrix, with creamy montmorillonite in the interstices. The top soil has been eroded away by the stream which emplaced the basal conglomerate.
1077.5–1088.3	Basalt	Solid basalt with large stretched vesicles typical of an aa lava. One unbroken core is 31½ inches long. The rock is nonporphyritic.
1088.3–1089	Basaltic clinker	Partly weathered red clinker.
1089–1097	Basaltic clinker	Red aa clinker.
1097–1107	Pahoehoe	Very vesicular olivine pahoehoe with slightly weathered surface.

TABLE 2

DESCRIPTION OF CORE FROM EWA NO. 2 HOLE

DEPTH (IN FEET)	ROCK TYPE	DESCRIPTIVE NOTES
0–10	Artificial fill	Crushed blue basalt and coral fill for drill platform.
10–18.8	Calcareous soil	Tan calcareous muddy soil with secondary calcified lumps.
18.8–36.5	Brown sandy soil	Chiefly basaltic grains; a few pebbles of basalt ¼ inch across. Some secondary calcite nodules. Changes to plastic brown clay downward.
36.5–46	Gray marl	Lumps of lime and concretions in gray mud; probably weathered surface of underlying reef.
46–102	Reef limestone	Hard reef limestone with shell molds, much recrystallized.
102–118	Reef detritus	Reef limestone with red mud in the interstices to 111 ft, and then changes to gray mud.
118–120	Brown sand	Fine silt and sand becoming coarser toward the bottom. Sand contains 50% well-rounded basaltic grains.
120–122	Coarse calcareous sand and gravel	Subangular reef detritus.
122–129	Brown mud	Fine mud. No lime present.
129–141	Indurated limy mud	Grayish-brown indurated mud with sharp break at top. Suggests very different environment. Contains tiny holes, possibly root holes with limonitic stain. Silty at 137–139 ft, with concretions. Some holes are lined with concentric structure.
141–161	Brown mud	Brown mud with mottled soil structure.
161–162	Brown silt and sand	Brown basaltic sand.
162–163	Brown mud	
163–165	White mud	White calcareous mud with some calcareous fragments; much recrystallized calcite with ⅛-inch crystals.
165–182	Reef limestone	Recrystallized reef limestone in fragments.
182–184	Limestone fragments in brown mud	Broken reef fragments in mud.
184–184.2	Black organic mud	
184.2–192	Brown mud	
192–194	Fine sand	Basaltic fine sand.
194–199	Brown mud	
199–204	Muddy fine sand	
204–208	Gravel and sand	Basaltic pebbles partly weathered in a sandy matrix.
208–239	Brown mud	Brown mud with pure calcite lumps ½ inch across.
239–241	Gravel and sand	Brown dirty basaltic sand with tiny round pebbles up to ¼ inch across.
241–262.5	Brown mud	
262.5–263	Sand and gravel	Brown nearly completely weathered basaltic gravel (¼ inch or less) and sand.
263–268	Brown mud	
268–271	Coarse sand	Coarse sand (basaltic) and mud.
271–274	Brown mud	Brown basaltic mud.
274–286	Brown and white mud	Brown mud with soft secondary lime deposits and irregular masses. A few hard calcite lumps. Lumps become more numerous at 285 ft.
286–288	Brown mud	
288–290	Fine sand	Fine basaltic sand and mud. Sand grains are mostly decomposed and have a variety of colors.

TABLE 2 (*Continued*)

DESCRIPTION OF CORE FROM EWA NO. 2 HOLE

DEPTH (IN FEET)	ROCK TYPE	DESCRIPTIVE NOTES
290–294	Brown mud	Brown basaltic mud.
294–297	Fine Sand	Brown basaltic sand and mud.
297–300	Brown mud	Brown basaltic mud.
300–301	Brown sand	Brown basaltic sand showing ⅛-inch and ¼-inch layers of coarse and fine sand.
301–307	Brown mud	Brown basaltic mud.
307–310	Fine sand	Brown basaltic sand and mud.
310–326	Brown mud	Brown basaltic mud, very mottled starting at 328 ft. Much limonitic from 333 to 334 ft along fractures.
326–330	Brown sand	Basaltic sand and silt much weathered.
330–339	Brown mud	Brown laminated mud.
339–344	Brown sand	Brown calcareous (secondary) sand, in places indurated with lime.
344–381	Brown silt and mud	Brown silt with soil structures in places.
381–400	White and gray marl	Mottled gray, white, and brown mud. Contains oyster shells and lime nodules.
400–415	Brown limestone	Recrystallized reef. At 405 ft 3 inches of brown mud mixed with coral fragments.
415–418	Brown marl and limestone	Fragments of recrystallized reef mixed with brown mud.
418–420	Brown and gray marl	Fragments of limestone mixed with brown and gray clay.
420–425	Gray limestone	Large fragments of limestone, probably recrystallized reef, oyster shells, etc., mixed with some gray and brown mud between 420 and 423 ft. At 423–425 ft large sections of limestone.
425–428	Gray-brown marl	
428–438	Brown mud (soil)	Plastic brown silty clay.
438–447	Gray marl	At 443 ft a 4-inch layer of red soil.
447–462	Brown mud (soil)	Stratified; soil structure contains well weathered basalt pebbles.
462–486	Brown muddy sand	At 467–469 ft and at other depths nearly pure coarse medium basaltic sand; remainder of section muddy sand; at 483–486 ft no sand, just brown mud.
486–499	Brown gray marl	Oyster shells abundant. The core from 487 to 498 ft was lost in a drilling mishap, but the cores at 487 and 498 ft were of the same lithology, and so possibly the missing 11 ft are also brown gray marl.
499–504	Brown silty mud	
504–517	Red basaltic, residual soil	Numerous highly weathered basalt cobbles; e.g., at 508, 510, 511, 512 ft, all about 4–6 inches. At 513 to 514.5 ft one large pahoehoe boulder 1½ ft in diameter was cored. From about 515 ft the soil grades imperceptibly into soft weathered aa basalt.
517–535	aa basalt	At 517 ft rotten aa basalt; no distinct upper surface; grades continually into soil above. From about 518 ft blue weathered aa basalt; large elongated vesicles.
535–542	aa clinker (soil)?	Weathered aa clinker, lower portion highly weathered into soil structures.
542–544	aa basalt	Blue, fractured, somewhat weathered aa basalt.

surface, the coral reef facies shifted landward, allowing the accumulation of a thick coralline limestone reef.

9. The growth of this reef was followed by a progradation of the lagoonal facies during which time nearly 100 ft of brown lagoonal mud accumulated. The upper surface of this mud is capped by several feet of bedded beach rock, indicating a still stand at —203 ft MSL.

10. Above the beach rock is another reef limestone section indicating a migration of coral facies landward again. After a short time this trend reversed itself, for at —160 ft MSL brown mud and soil occur, indicating a progradation of the lagoonal facies. Both of the above two unconformities may correspond with the Penguin Bank stand of the sea.

11. Above this level the coral reef facies advanced inland and dominated the remaining portion of the core except for one soil horizon at —38 ft MSL that may correspond to the Waipio stand of the sea.

12. The reef making up the present surface of the Ewa Plain appears to belong to the Waimanalo + 25-ft stand of the sea, inasmuch as reef limestone can be traced from Ewa No. 1 to Ewa No. 2 where it overlies lagoonal muds. The surface of this reef probably has been eroded by the sea as it retreated from the + 25-ft level to the last glacial low stand.

CURRENT RESEARCH AND FUTURE PLANS

It will be several years before the Ewa cores have been thoroughly examined. Even then the cores will continue to be used for comparison with cores obtained elsewhere. The interpretation of results of the preliminary core examination, especially of those sections dealing with the geologic history, doubtless will be modified as the research proceeds. The cores are stored at the Hawaii Institute of Geophysics, University of Hawaii, Honolulu.

The present plans for the examination of the Ewa cores include palaeontologic, mineralogic, and chemical analyses of selected samples along the core. Specifically the following types of studies are currently underway:

1. Soil analyses. Chemical and mineralogic studies of samples from suspected soil hori-

zons; climatic and other environmental interpretations of proven soils.

2. Geochemical analyses. Absolute dating of various horizons within the cores by means of radioactive decay of certain elements. Methods used will include K-Ar, C^{14}, and a new helium method. Paleo-temperature measurements will also be made.

3. Palaeontologic analyses. Macro- and micro-palaeontologic studies of fauna and flora; determinations of geologic age by the use of these fauna and flora; paleoecologic studies.

4. Sedimentologic analyses. Textural studies of the sediments and sedimentary rock; studies of the sedimentary environments.

5. Mineralogic and petrologic analyses. Optical, chemical, and X-ray determinations of minerals and rocks, including analyses of the underlying basalts.

The results of these analyses will give a partial answer to such questions as the tectonic history of the Hawaiian Archipelago and the nature and magnitude of the eustatic changes in sea level recorded in the Ewa cores. However, additional information will be necessary before the complete stratigraphic and paleoecologic history can be unravelled. Most of the sediments in the Ewa cores indicate either a lagoonal or back reef environment. A very extensive barrier reef undoubtedly lay to seaward of the present Ewa sites throughout most of the geologic period recorded in the cores. Without cores through this reef the stratigraphic interpretation of the present Ewa cores is handicapped. Consequently, plans are underway for a research program to drill two more holes in the Ewa area, both offshore and in the area of the anticipated barrier reef. The first hole would be drilled in about 400 ft of water three miles off the beach along the 158th meridian. This deeper hole would be drilled over the 1,800-ft shelf, possibly Miocene in age (Menard et al., 1962). Sediment thickness in this area is about 2,000 ft, based on seismic work.

With the complete cores recovered from these two offshore holes it would be possible to trace completely the sedimentary facies changes from terrestrial to lagoonal to barrier reef both horizontally and vertically throughout the Pleistocene Epoch and possibly the later Tertiary Period.

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The Larval Development of the Crab, *Cyclograpsus cinereus* Dana, under Laboratory Conditions[1]

John D. Costlow, Jr.[2] and Elda Fagetti[3]

EARLY DESCRIPTIONS of larvae of the Grapsidae, based largely on material from the plankton and frequently limited to the first zoeal stage, suggested considerable uniformity in the morphological characteristics of larvae of this group of crabs (Hyman, 1924). Subsequent descriptions, based on plankton material as well as on material obtained from rearing the larvae in the laboratory, have served to point out certain differences which do exist in the larvae of this group (Aikawa, 1929; Hart, 1935). To date, however, a very limited number of larvae of crabs belonging to the family Grapsidae have been described.

Within the subfamily Sesarminae larvae of two species of the genus *Sesarma* have been described from rearing under laboratory conditions (Costlow and Bookhout, 1960, 1962). These two species, *S. cinereum* and *S. reticulatum*, while relatively common along the east coast of North America and even extending as far as Venezuela, are not known from the west coast of North or South America.

On the west coast of Chile, crabs of the subfamily Sesarminae are limited to two species of *Cyclograpsus*: *C. cinereus* Dana and *C. punctatus* Milne Edwards (Garth, 1957). The larvae of these species have not been described, either from rearing or from the plankton, and nothing is known about the effect of environmental factors on the development of the larval stages.

The present study has had two main objectives: one, to rear the larvae of *Cyclograpsus cinereus* Dana and provide a description of all developmental stages; and two, to determine if salinity and temperature affect the survival and duration of the larval stages.

METHODS

Ovigerous *Cyclograpsus cinereus* females were obtained in the vicinity of the Marine Biological Station, Montemar, University of Chile, and flown by air to the Duke University Marine Laboratory, Beaufort, North Carolina. The crabs were transported in sea water, salinity 34.4 ppt, and extreme temperature changes were avoided by packing them in thermos containers. On arrival at Beaufort, the females were retained at 35 ppt, 20°C. At the time of hatching the larvae were removed, segregated into series of 50 or 100 larvae, and maintained at the temperature-salinity combinations shown in Table 1. Within each temperature-salinity series the larvae were further subdivided, 10 zoeae per bowl, and were fed *Artemia* nauplii and *Arbacia* eggs. Each day the larvae were moved to freshly filtered sea water in clean bowls and fresh food was added. At this time the bowls were examined for exuviae, the dead larvae were removed, and the number was recorded. When the megalops stage was reached the larvae were maintained individually in plastic compartmented boxes and fed only *Artemia* nauplii.

From mass cultures the larvae and exuviae were preserved in 5% formalin at known stages of development. Drawings were made to scale with the aid of a camera lucida and the chromatophore pattern was determined from living larvae.

RESULTS

Larval Stages

There are five zoeal stages and one megalops stage in the complete development of *C. cinereus*. The major characteristics of each larval stage are as follows:

FIRST ZOEA (Fig. 1, *A–I*): The cephalothorax has a gibbose dorsal spine which curves caudally (Fig. 1, *A*). The rostral spine is short and the carapace is devoid of lateral spines.

TABLE 1

COMPARISON OF ORIGINAL NUMBER OF LARVAE OF *Cyclograpsus cinereus,* MAINTAINED AT DIFFERENT
COMBINATIONS OF SALINITY AND TEMPERATURE, SURVIVAL TO MEGALOPS AND CRAB STAGE, AND
TIME REQUIRED FOR DEVELOPMENT THROUGH ALL LARVAL STAGES

SALINITY (ppt)	TEMP. °C	ORIGINAL NUMBER	PERCENT TO MEGALOPS	PERCENT TO CRAB	TIME OF DEVELOPMENT (DAYS)		
					HATCH TO MEGALOPS	MEGALOPS DURATION	HATCH TO CRAB
30	20	100	70.0	45.0	24–33 **25.7**	15–31 **20.3**	40–57 **45.7**
35	20	100	61.0	38.0	25–29 **26.0**	15–29 **22.0**	40–56 **47.7**
30	25	50	30.0	2.0	19–24 **20.7**	13	30
35	25	50	44.0	10.0	18–21 **19.7**	14–16 **15.0**	33–35 **34.2**
35	30	50	0.0	0.0	—	—	—

* Average figures given in bold type.

The eyes are not stalked. The ventrolateral edge of the carapace bears 8 small spines. The abdomen (Fig. 1, *B*) consists of 5 segments plus the telson. The second abdominal segment has a short lateral hook directed anteriorly. The telson formula is 3 plus 3 spines and the furcal rami are denticulate.

The antennule (Fig. 1, *C*) bears 2 long aesthetes and 2 shorter, unequal setae. The antennal peduncle (Fig. 1, *D*) is unsegmented and terminates as a large, denticulate spine. The exopodite is shorter and terminates as 2 unequal spines. The bisegmented endopodite of the maxillule (Fig. 1, *F*) bears 4 terminal setae, 1 subterminal seta on the second segment and a single seta on the first segment. The basipodite has 5 terminal plumose spines and the coxopodite bears 4 terminal and 1 subterminal setae. Four unequal soft, plumose setae fringe the distal border of the scaphognathite of the maxilla (Fig. 1, *G*), and the apical tip terminates as 1 plumose hair. The bilobate endopodite bears 2 plumose setae on each lobe and its margins are covered with numerous fine hairs. The bilobed coxopodite and basipodite bear 5-4 and 2-4 plumose setae respectively. The basopodites and exopodites of maxillipeds one and two are as shown in Figure 1, *H* and *I*. The 5-segmented endopodite of the

first maxilliped has a setation of 2,1,1,2,5 (Fig. 1, *H*). The 3-segmented endopodite of the second maxilliped (Fig. 1, *I*) has a setation of 0,1,5.

The pattern of chromatophores is consistent for all five zoeal stages. The location of melanophores in the carapace is as follows: (a) 1, median and dorsal to eyes; (b) 1 pair, ventrolateral border; (c) 1 pair, median-lateral, posterior margin. Melanophores of the zoeal appendages are as follows: 1 at basis of the antenna; 1 in mandible; 1 in labrum; and 1 in basipodite of first maxilliped. In the abdominal segments 1 melanophore is found dorsal to the gut in segments one through four, 1 in the midventral region of segments two through five (in first and second zoea), and through six (in third to fifth zoea), and 1 pair in the posterior-lateral corner of segment five.

SECOND ZOEA (Fig. 2, *A–I*): The eyes are stalked, the dorsal spine is no longer gibbose, and the lateral spines are present (Fig. 2, *A*). The ventrolateral borders of the carapace bear 6 small spines plus 6 setae and there are 2 spines on the posterior, middorsal margin. Antennule now bears 4 aesthetes, approximately equal in length (Fig. 2, *C*). Changes in setation of the appendages are limited to the following: basipodite of maxillule has 5 spines

Fig. 1. Side view (A) of first zoeal stage of *Cyclograpsus cinereus* Dana. B, Ventral view of abdomen; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped.

plus 2 setae and a spine projects from the protopodite (Fig. 2, F). Scaphognathite of maxilla (Fig. 2, G) has 5 proximal and 3 distal plumose setae. Setation of the exopodite of the first and second maxillipeds has increased to 6 (Fig. 2, H and I). Setation of the endopodite of the first maxilliped is now 2,2,1,2,5, and of the second maxilliped, 0,1,6.

THIRD ZOEA (Fig. 3, A–I): Small spines on the ventrolateral borders of the carapace have decreased to 5 and setae increased to 10 (Fig. 3, A). The sixth abdominal segment is added and the number of telson spines has increased to 8 on the inner surface (Fig. 3, B). Changes in setation of the appendages are limited to the

following: 1 small spine is added on the lateral margin of basopodite of maxillule (Fig. 3, F); scaphognathite of maxilla has 8 proximal and 6 distal plumose setae and each lobe of basopodite bears 5 setae (Fig. 3, G); 1 seta has been added to lateral margin of coxopodite of maxilla (Fig. 3, G). Setation of exopodite of first and second maxillipeds has increased to 8 (Fig. 3, H and I). Setation of endopodite of first maxilliped is now 2,2,2,2,5.

FOURTH ZOEA (Fig. 4, A–I): Small spines on ventrolateral borders of carapace decreased to 4 and setae increased to 14. Rudiments of pereiopods present under carapace (Fig. 4, A). Dorsal surface of first abdominal segment now
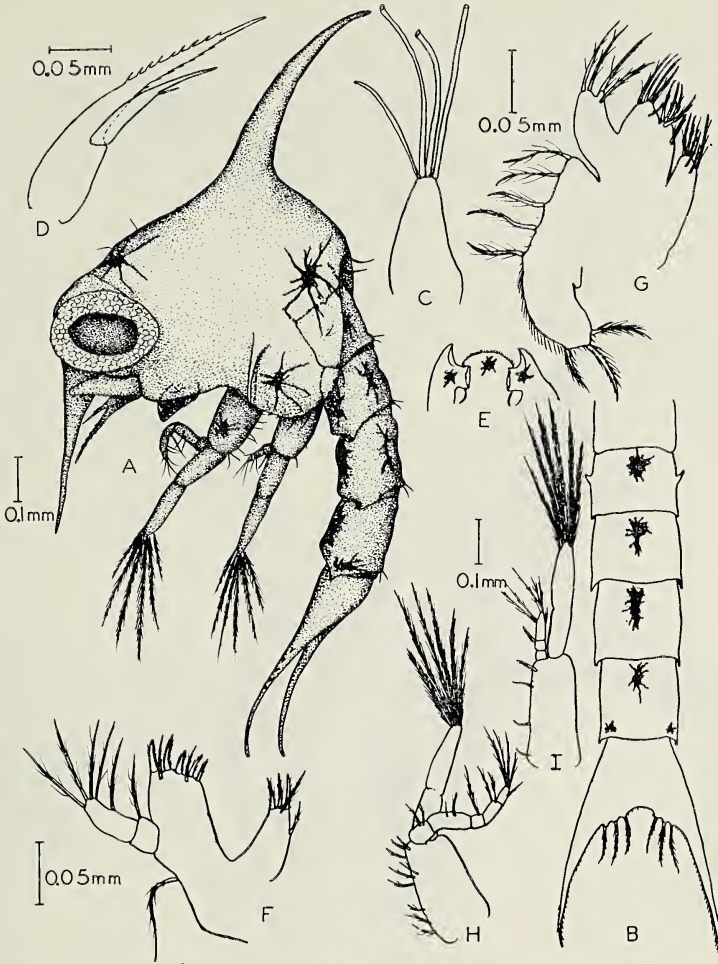
FIG. 2. Side view of (*A*) of second zoeal stage of *Cyclograpsus cinereus* Dana. *B*, Ventral view of abdomen; *C*, antennule; *D*, antenna; *E*, mandible; *F*, maxillule; *G*, maxilla; *H*, first maxilliped; *I*, second maxilliped.

bears 5 spines and pleopod buds are present on segments two through six (Fig. 4, *B*). Setation of the appendages is as follows: antennule (Fig. 4, *C*) bears 5 terminal and 1 subterminal aesthetes; the unsegmented endopodite bud of the antenna (Fig. 4, *D*) is approximately half the length of the antennal spine. Setation of basopodite of maxillule has increased to 11 (Fig. 4, *F*). Scaphognathite of maxilla (Fig. 4, *G*) has 16 proximal and 9 distal plumose setae and setation of coxopodite has increased to 9. Setation of exopodite of first and second maxillipeds (Fig. 4, *H–I*) has increased to 10. Setation of endopodite of first maxilliped is now 2,2,2,2,6 (Fig. 4, *I*).

FIFTH ZOEA (Fig. 5, *A–I*): Minute spines on ventrolateral borders of carapace increased to approximately 10, and 18 setae are present (Fig. 5, *A*). Rudiments of unsegmented pereiopods now visible under carapace. Pleopods of abdominal segments two through six partially segmented (Fig. 5, *B*). Changes in setation of the appendages are as follows: swollen basal region of antennule (Fig. 5, *C*) bears 2 small, plumose setae, endopodite bud is present and subterminal aesthetes have increased to 4. Endopodite of antenna (Fig. 5, *D*) partially segmented and longer than exopodite. Setation of basopodite of maxillule (Fig. 5, *F*) increased to 13 and coxopodite now bears 9 setae.
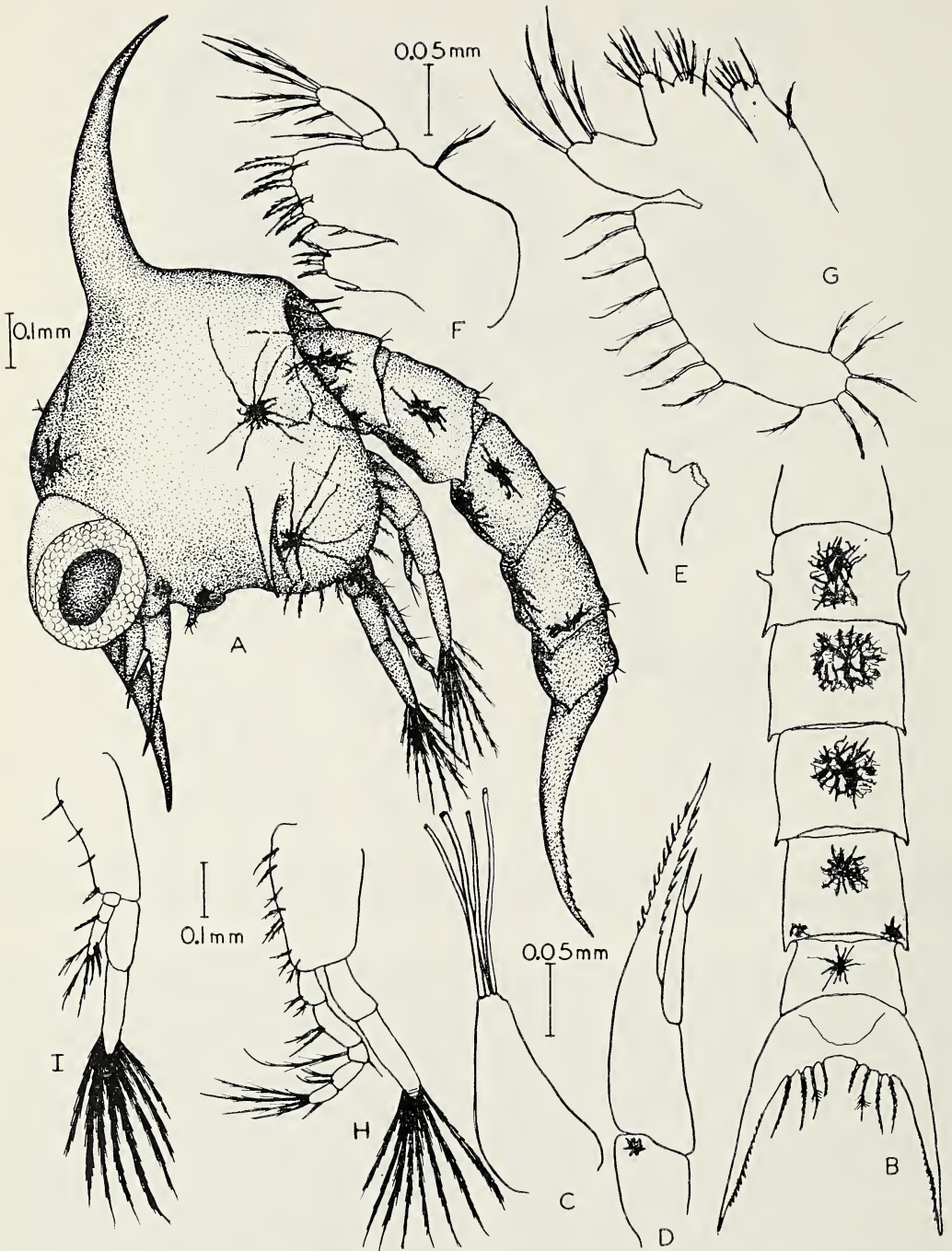
FIG. 3. Side view (*A*) of third zoeal stage of *Cyclograpsus cinereus* Dana. *B*, Ventral view of abdomen; *C*, antennule; *D*, antenna; *E*, mandible; *F*, maxillule; *G*, maxilla; *H*, first maxilliped; *I*, second maxilliped.
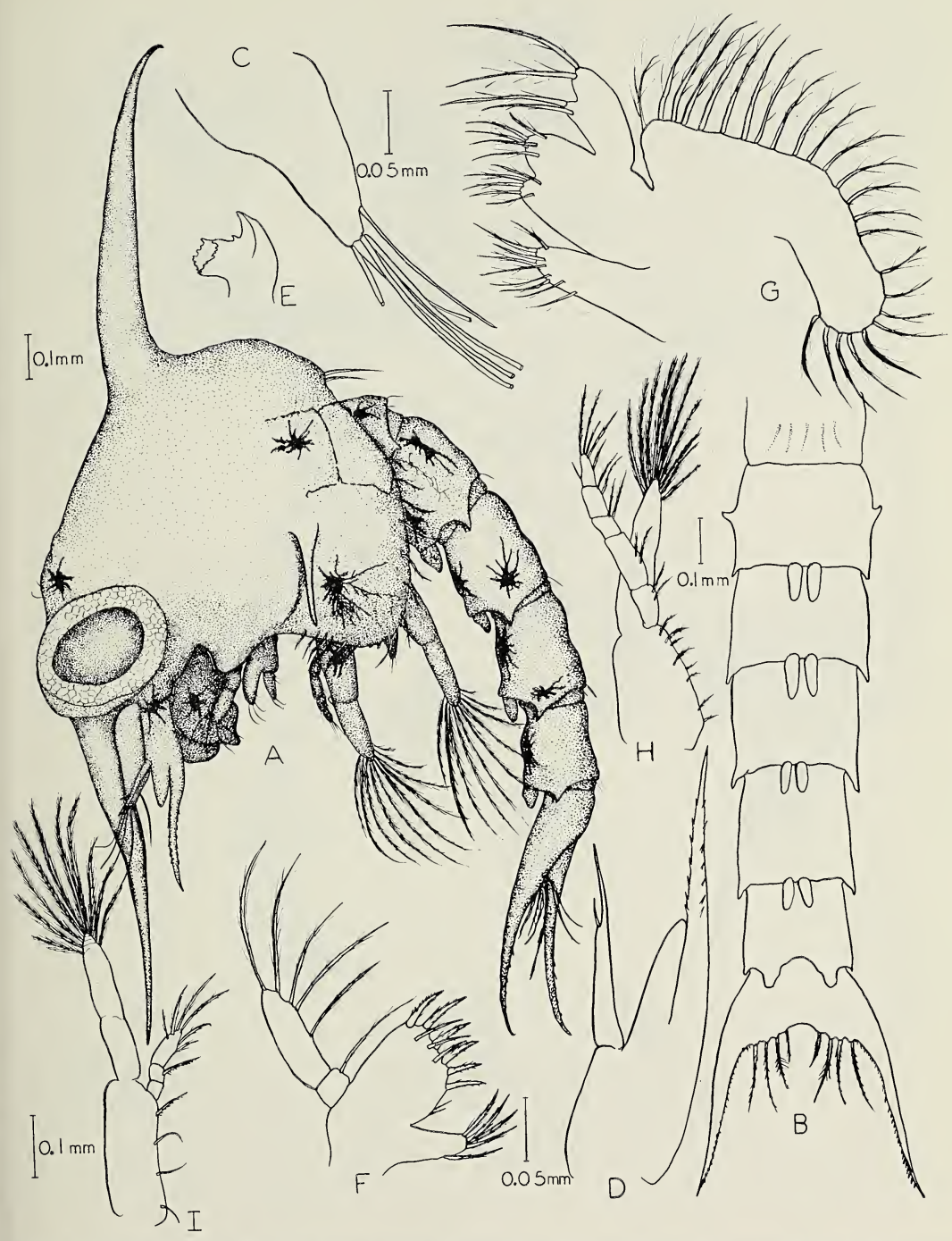
Fig. 4. Side view (*A*) of fourth zoeal stage of *Cyclograpsus cinereus* Dana. *B*, Ventral view of abdomen; *C*, antennule; *D*, antenna; *E*, mandible; *F*, maxillule; *G*, maxilla; *H*, first maxilliped; *I*, second maxilliped.
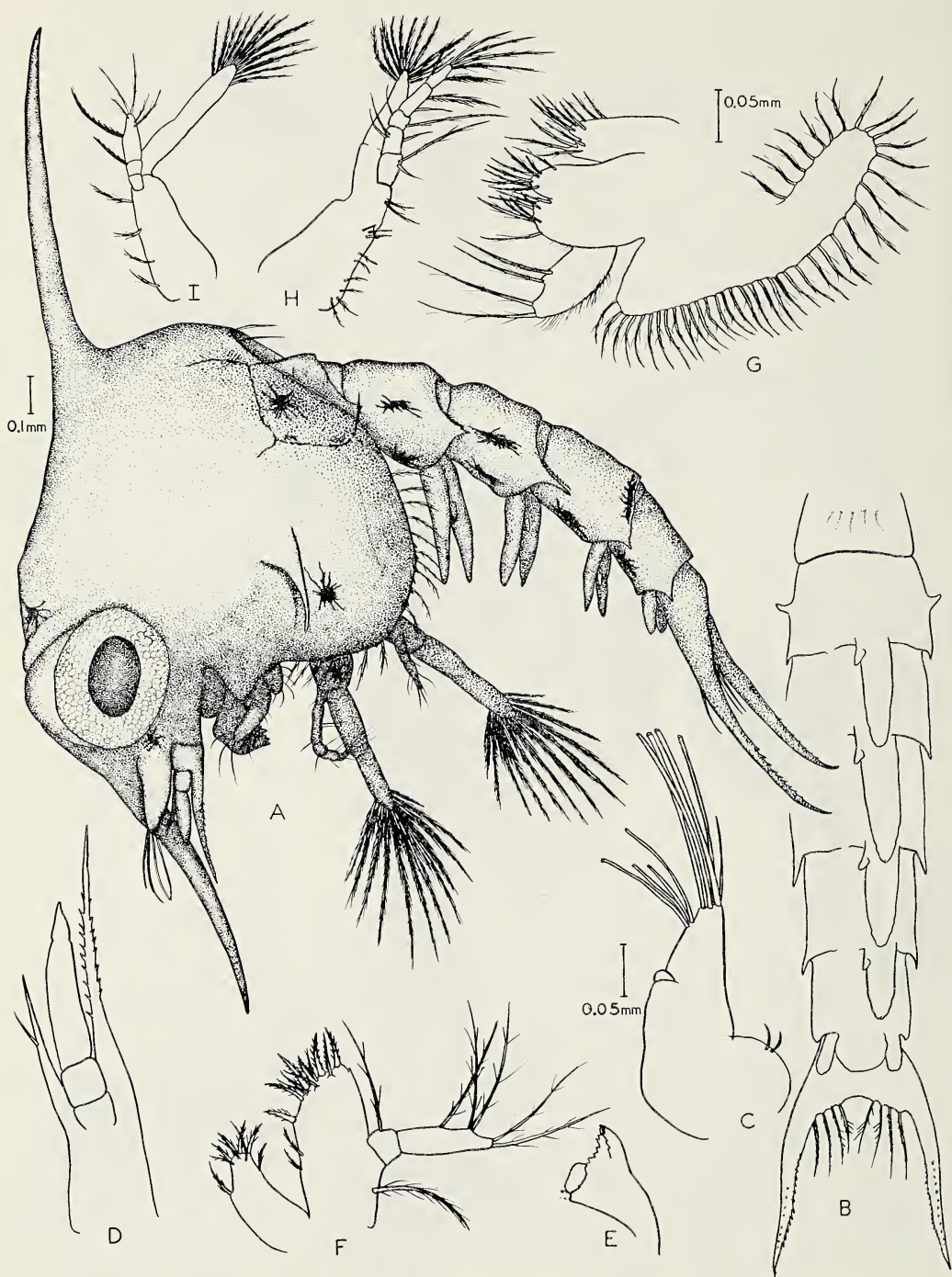
FIG. 5. Side view (*A*) of fifth zoeal stage of *Cyclograpsus cinereus* Dana. *B*, Ventral view of abdomen; *C*, antennule; *D*, antenna; *E*, mandible; *F*, maxillule; *G*, maxilla; *H*, first maxilliped; *I*, second maxilliped.
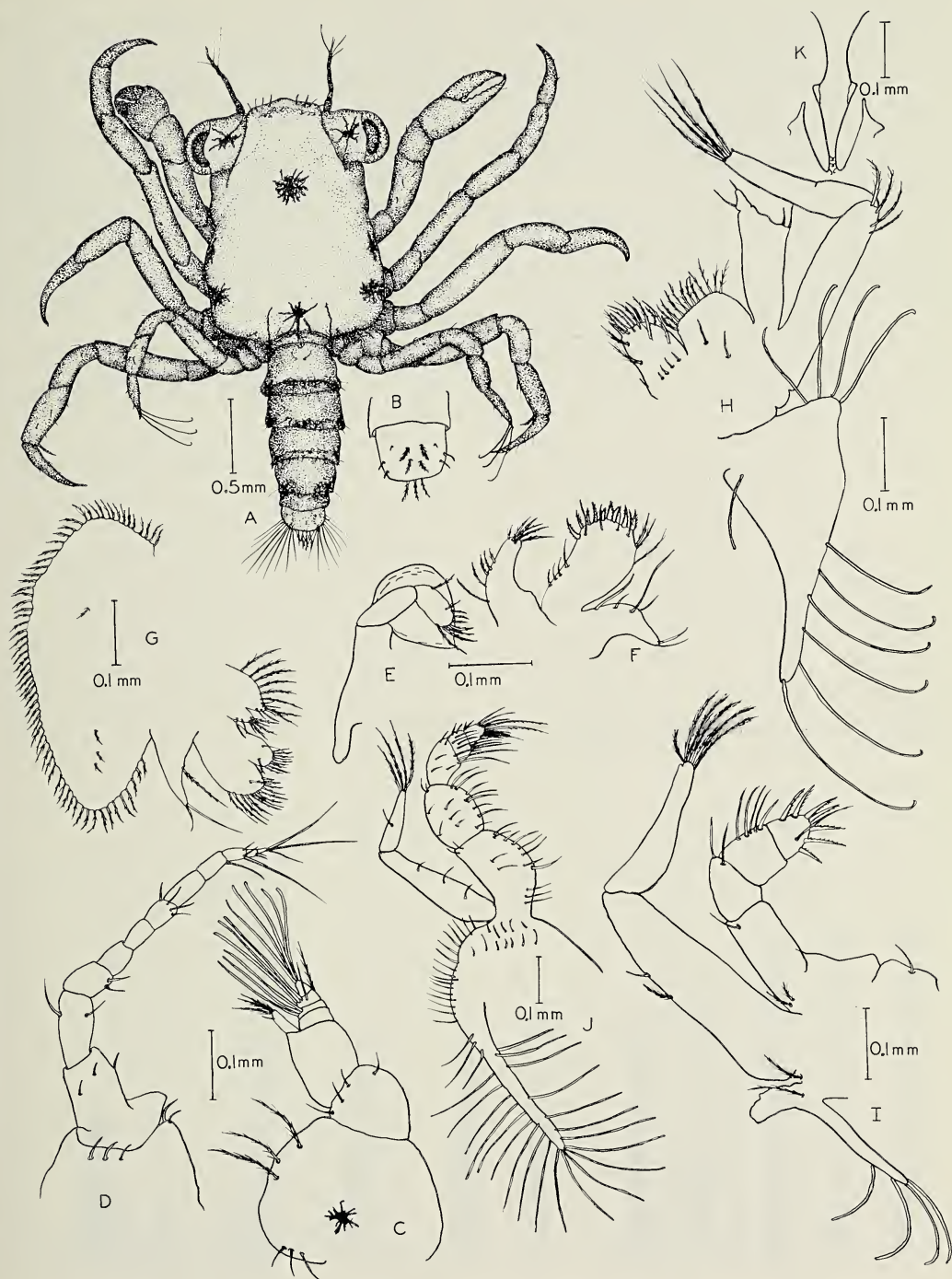
Fig. 6. Dorsal view (*A*) of megalops of *Cyclograpsus cinereus* Dana. *B*, Telson; *C*, antennule; *D*, antenna; *E*, mandible; *F*, maxillule; *G*, maxilla; *H*, first maxilliped; *I*, second maxilliped; *J*, third maxilliped; *K*, pleopods.

Scaphognathite of maxilla (Fig. 5, *G*) has approximately 30 proximal and 12 distal plumose setae, setation of basopodite increased to approximately 16, and the coxopodite now bears 11 setae. Setation of exopodite of first and second maxillipeds (Fig. 5, *H–I*) has increased to 12. Setation of endopodite of first maxilliped is now 2,3,2,2,6.

MEGALOPS (Fig. 6, *A–K*): Cephalothorax without rostral spines and provided with hairs at lateral edges (Fig. 6, *A*). Abdomen 6-segmented, with telson (Fig. 6, *B*) bearing 4 dorsal and 3 terminal plumose setae. Antennule (Fig. 6, *C*) with 2 flagella on second segment. Unsegmented flagellum with 3 terminal setae and 1 subterminal seta. The 4-segmented flagellum bears 3 aesthetes on the second segment, 4 aesthetes plus 1 seta on the third segment, and 5 aesthetes on the terminal segment. Antenna (Fig. 6, *D*) with 11 segments and setation as shown in Figure 6, *D*. Mandible (Fig. 6, *E*) with 2-segmented palp bearing 9 plumose setae on terminal segment. Unsegmented endopodite of maxillule (Fig. 6, *F*) with 2 terminal and 4 lateral setae. Basopodite with approximately 21 spines and setae and the coxopodite with 6 terminal and 5 lateral setae. Scaphognathite of maxilla (Fig. 6, *G*) fringed with approximately

70 plumose setae (Fig. 6, *G*). Unsegmented endopodite bearing 2 unequal terminal setae and 1 subterminal plumose seta. Lobes of basopodite bearing 13 and 11 plumose setae, respectively, and lobes of coxopodite with 6 and 12 setae. The first, second, and third maxillipeds are as shown in Figure 6, *H, I,* and *J*. Setation of exopodites of pleopods of abdominal segments two to five varies from 17 to 20. Endopodites of all pleopods have 3 median hooks (Fig. 6, *K*). Uropods bisegmented with 1 seta on first segment and 10 setae on second segment.

Chromatophore pattern of carapace as follows: one, dorsomedian surface, one on each median-lateral border, a pair on ventral surface of rostrum, joined at the median line, and one at each posteriolateral corner. Chromatophore pattern of appendages: one on each eyestalk, one on basopodite of antennule, one on basopodite of cheliped, mandibles, and labrum. Within the abdominal segments melanophores are located as follows: one in first segment, dorsal to gut, extending into cephalothorax; one at posterioventral margin of segments two through five, the chromatophore of segment five extending into proximal region of segment six.
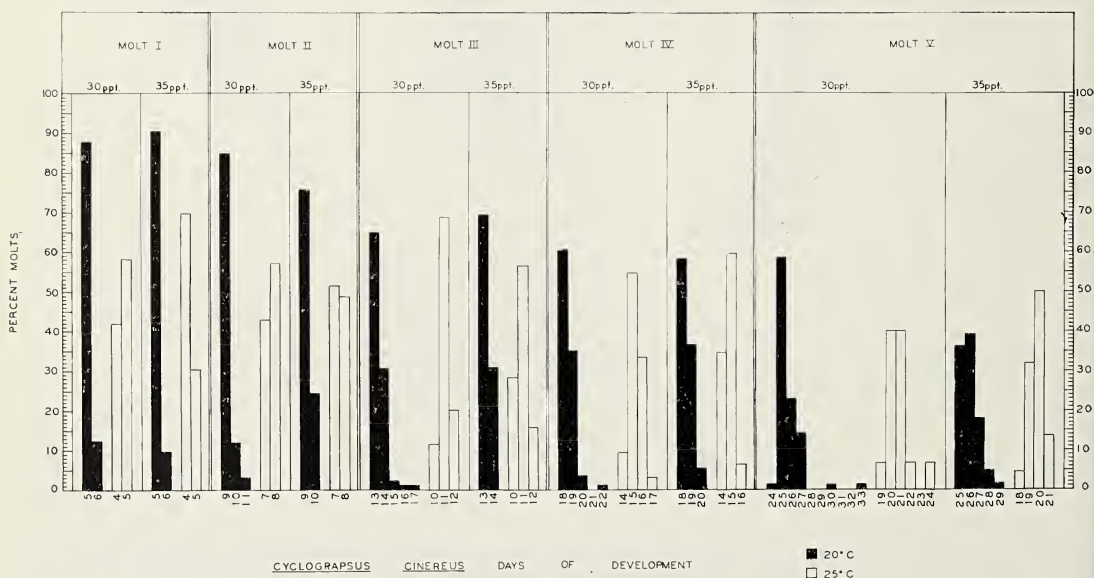
FIG. 7. Comparison of the time of larval molts for zoeae and megalops of *Cyclograpsus cinereus* Dana reared in the laboratory at different salinities and temperatures. *Black,* 20°C; *white,* 25°C.

Larval Development

The frequency of molting during the five zoeal and one megalops stages is shown in Figure 7. The first and second molts of most larvae were confined to two days at all four salinity-temperature combinations. By the time of the third molt, however, the uniformity was not as apparent and the later molts were spread over three, four, and five days. Figure 8 shows the time required for development of the five zoeal stages and megalops of *C. cinereus* when maintained at combinations of two salinities and two temperatures. At 20°C, the duration of all larval stages is longer than that observed for larvae reared at 25°C. This difference is more pronounced as development continues and is quite apparent for the megalops stage. Within the two salinities used, 30 and 35 ppt, there is no apparent difference in the time required for development of the larval stages (Fig. 8). The average time for total development to the first crab (Fig. 8) at 25°C was 30 days at 30 ppt and 34.2 days at 35 ppt. At 20°C and 30 ppt, 45.7 days were required and at the same temperature and 35 ppt comparable development required 47.7 days.

Mortality of the individual larval stages is shown in Figure 9. Although larvae were main-
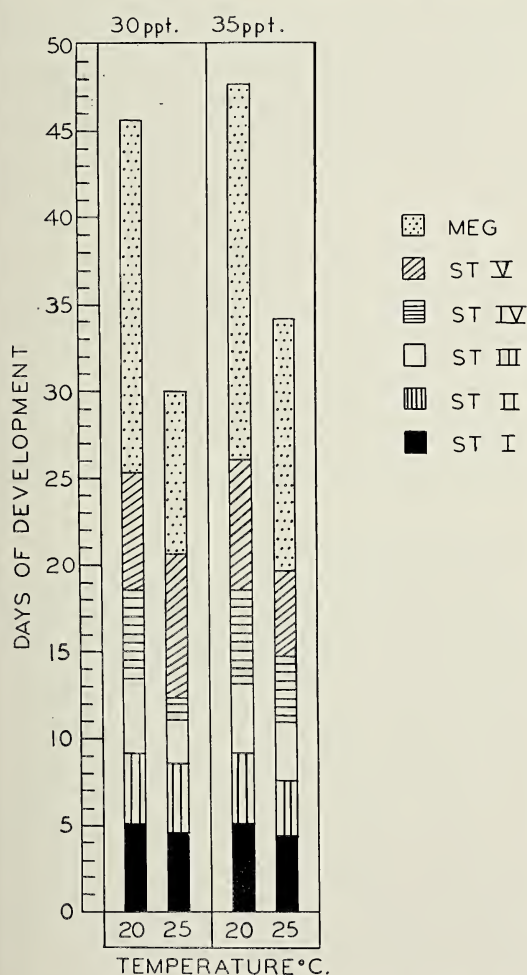
FIG. 8. Comparison of the duration of five zoeal stages and megalops of *Cyclograpsus cinereus* Dana reared in the laboratory at different salinities and temperatures.
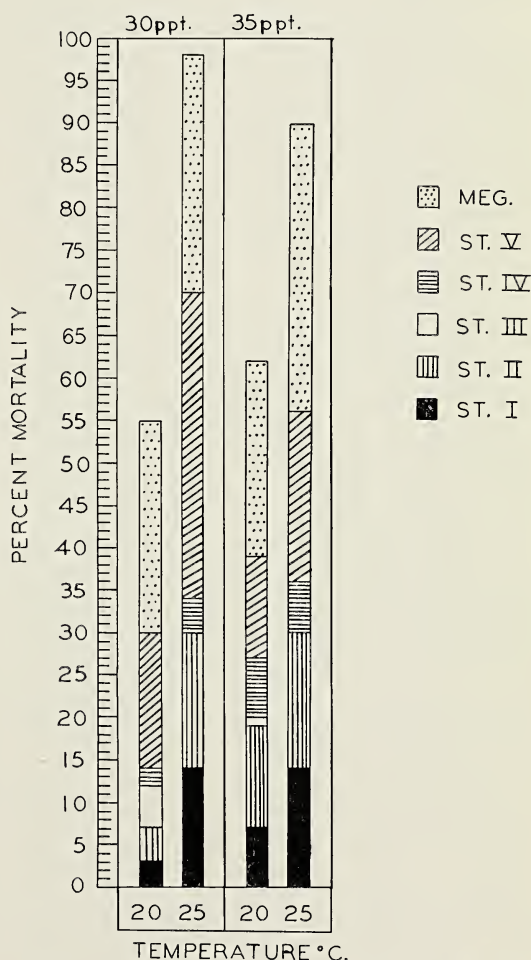
FIG. 9. Comparison of the mortality of the five zoeal stages and megalops stage of *Cyclograpsus cinereus* Dana reared in the laboratory at different salinities and temperatures.

tained at 30 and 35 ppt, 30°C, all died within the first two days following hatching and are not included in Figure 9. Mortality of most larval stages was higher at 25°C than at 20°C. Mortality of any one zoeal stage at 20°C does not exceed 16%, while at 25°C mortality within one stage (Stage V) was as high as 36%. At 25°C, there was a tendency for the mortality to be higher in the later larval stages than in the early zoeal stages. Survival to the crab ranged from 2 to 10% at 25°C and from 38 to 45% at 20°C.

DISCUSSION

Larval Stages

A comparison of the larvae among species of the same subfamily as *Cyclograpsus cinereus* is limited to descriptions of *Sesarma cinereum* (Hyman, 1924; Costlow and Bookhout, 1960), *Sesarma reticulatum* (Hyman, 1924; Costlow and Bookhout, 1962) and *Sesarma picta* (Aikawa, 1937). The number of zoeal stages varies considerably within those species of Sesarminae which have been described. *C. cinereus* has five zoeal stages, *S. cinereum* has four zoea (Costlow and Bookhout, 1960) and *S. reticulatum* has three zoeal stages (Costlow and Bookhout, 1962). Aikawa (1937), while describing the first stage zoea of *S. picta* from the plankton, does not indicate the total number of larval stages of this species. The first zoea of *C. cinereus* is quite distinctive in that the dorsal spine is gibbose. In all subsequent zoeal stages, when the dorsal spine is straight only *C. cinereus* has lateral spines. All the larval stages of *C. cinereus* may be further differentiated from zoeae of the three species of *Sesarma* by the absence of a knob on each lateral surface of the third abdominal segment of larvae of *C. cinereus*.

Among the Chilean species of the family Grapsidae the larvae of only one, *Grapsus grapsus* L., have been described to date (Aikawa, 1937). Only the first zoea was described and may be differentiated from the first zoeal stage of *C. cinereus* by the presence of the lateral knob on the third abdominal segment of *G. grapsus* as well as by the gibbose dorsal spine of *C. cinereus*.

The megalops of *C. cinereus* differs from the megalops of *S. cinereum* and *S. reticulatum* in several respects. The main differences can be observed in the rostrum, telson, antennule, and second maxilliped. The rostrum of *C. cinereus* megalops is not depressed as in *S. cinereum* (Costlow and Bookhout, 1960), and does not have a rostral spine as in *S. reticulatum* (Costlow and Bookhout, 1962). The telson of *C. cinereus* bears only 3 setae on the distal margin, while the telsons of *S. cinereum* and *S. reticulatum* bear 8 setae and 6 setae, respectively, plus lateral spines. In *C. cinereus* the unsegmented flagellum of the antennule is present, while in *S. cinereum* and *S. reticulatum* the unsegmented flagellum is absent and replaced by a single seta. The epipodite of the second maxilliped is present in the megalops of *C. cinereus* but absent in *S. cinereum* and in *S. reticulatum*.

Of all the other megalops of the family Grapsidae which have been described to date, none are found in Chilean waters. However, it should be noted that the megalops of *C. cinereus* bears a greater resemblance to megalops of *Hemigrapsus nudus* and *H. oregonesis*, which belong to the subfamily Varuninae and were described from the Pacific coast of Canada by Hart (1935), than to megalops of the subfamily Sesarminae.

A more detailed comparison of the morphology of larvae of *C. cinereus* with larvae of other closely related forms in Chilean waters must await additional descriptions.

Larval Development

The adults of *C. cinereus* are normally confined to the area from Ancon, Peru to Calbuco, Chile on the western coast of South America (Garth, 1957). One extra limital locality, Panama, has also been recorded (Rathbun, 1910, 1918). The habitat of the adults is in the upper level of the intertidal region, where they live under stones in the coarse sand. Ovigerous females have been observed in the Montemar region throughout the year with the exception of February. The principal spawning period, however, appears to be from July through November, when more than 60% of the population is ovigerous. During this period the water temperature increases from 12°C to 14°C. The salinity of the water in which larval development occurs is quite stable, ranging

from 34.1 ppt to 34.5 ppt (Antezana, Fagetti, and Lopez, 1965).

In the experimental conditions of the laboratory, duration of the five zoeal stages and one megalops stage appears to be relatively unaffected by the limited range of salinity used. The larvae did develop to the crab faster at 25°C than at 20°C, as would have been expected. Survival, however, was consistently higher at 20°C than at 25°C or at 30°C. The larval development of certain other species of Brachyura, normally considered to be estuarine, has been shown to be directly affected by salinity (Costlow and Bookhout, 1962; Costlow, Bookout, and Monroe, 1960, 1966). The results of the present study, however, suggest that the development of larvae of *C. cinereus* is not strongly influenced by the relatively small salinity fluctuations to which the larvae would be subjected during their planktonic existence in the waters off the western coast of Chile and Peru.

SUMMARY AND CONCLUSIONS

The larval stages of *Cyclograpsus cinereus* Dana have been reared in the laboratory from hatching to the first-stage crab. The larvae were maintained in combinations of three temperatures, 20°C, 25°C, and 30°C, and two salinities, 30 ppt and 35 ppt, and were fed recently hatched *Artemia* nauplii and fertilized *Arbacia* eggs.

There are five zoeal stages and one megalops under laboratory conditions. The larvae, as well as the setation of the functional appendages, have been described and figured. Descriptions of larvae of closely related species from Chilean waters are not available, but the larvae of *C. cinereus* Dana can be differentiated from the other grapsid larvae described to date.

Approximately 46 days were required for development to the crab at 20°C. At 25°C, development was completed in 30 to 34 days.

Larvae completed development to the first crab in salinity-temperature combinations other than 35 ppt, 30°C. A higher percentage of the

larvae survived at 20°C than at 25°C. Survival at 30 ppt and 35 ppt was simliar, suggesting that development under natural conditions is not affected by minor fluctuations in salinity.

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A Comparison of Euphausiid Shrimp Collections Made with a Micronekton Net and a One-Meter Plankton Net[1]

CHARLES W. JERDE

IN AN EVALUATION of variable factors affecting the apparent geographic range and estimated abundances of euphausiids, Brinton (1962) compared euphausiid catching ability of a 1-m diameter net, made principally of 0.65 mm mesh, with a 45-cm diameter net made of 0.33 mm mesh. He found that adult and juvenile euphausiids were taken by the larger net in numbers as great or greater than were obtained with the 45-cm net, but that only about half as many larvae were taken with the coarser meshed meter net as with the 45-cm net. Collections with the 45-cm net contained almost as many species as the collections with the 1-m net, which filtered a volume of water 5 times as great (Brinton, 1962).

On Scripps Tuna Oceanography Research cruises 64-1 and 64-2 (off southern Baja California) an attempt was made to sample consecutively to the same depth with a micronekton net and a 1-m diameter plankton net, in order to compare euphausiid catches between the two nets. This paper is an evaluation of the euphausiid catching ability of the two nets.

The author is indebted to Dr. Edward Brinton for his assistance in the identification of the euphausiids. The constructive advice of Dr. Maurice Blackburn, Dr. E. W. Fager, Dr. Milner B. Schaefer, and Dr. Paul Smith was gratefully received.

METHODS

A description and figures of the micronekton net are found in Blackburn and associates (1962); the net with a 2.3 m² mouth opening

is made of nylon netting of uniform mesh (apertures measuring about 5.5 mm by 2.5 mm) throughout and has a detachable cod end of #56 XXX grit gauze (mesh aperture 0.31 mm). The micronekton net was towed in oblique hauls, from an average depth of 131 m to the surface at 5 knots for an average period of 50 minutes; depth of haul was determined by a bathythermograph attached to the upper edge of the square mouth opening (1.5 m by 1.5 m). A flow meter was not used with the micronekton net, and volume of water filtered was estimated from size of mouth opening, ship speed, duration of tow, and a filtration coefficient of 0.757 which had been determined by Blackburn (MS). Estimated volume of water filtered per tow with the micronekton net ranged from 14,000 to 16,000 m³.

The 1-m net (Ahlstrom, 1948) has a mouth opening of 0.785 m² and is made of #30 XXX grit gauze (mesh 0.65 mm) in the forward section of the net, with #56 XXX grit gauze (mesh 0.31 mm) in the rear section and cod end. It was towed in oblique hauls, from an average depth of 133 m to the surface at 1–2 knots for an average period of 14 minutes. Maximum depth of haul of the 1-m net was estimated from the amount of wire out and the wire angle; a calibrated flow meter placed at the center of the mouth opening was used to estimate volume of water filtered, which ranged from 385 to 468 m³. On the average, the micronekton net filtered 34.4 times as much water as the meter net at each station.

Euphausiids were picked from the entire collection of each tow at 10 stations. "Wet" displacement volume of each entire euphausiid sample was determined according to the method of Ahlstrom and Thrailkill (1963). All euphausiids in these plankton samples were counted, with the exception of those in cruise 64-2 collections at stations 41 and 56; from these two collections, aliquots of ½ and ¼, respectively,

were counted. Because the samples taken with the micronekton net were very large, it was necessary to use aliquots in all cases; these aliquots ranged from 2.75% to 50% depending upon the size of the sample. A Folsom plankton splitter (McEwen, Johnson, and Folsom, 1954) was used for fractionating the samples, with the exception of the micronekton sample at station 41. For this sample the animals in a gallon jar were kept in suspension by agitation, and a portion of animals and fluid was poured out; "wet" displacement volume of the animals was determined, and subsequently the euphausiids were measured and counted.

After the actual catch of euphausiids was estimated, the numbers were standardized for each size category to numbers per 500 m³ of water (Table 1). Blackburn (MS) estimates that the amount of water actually filtered by the micronekton net at a speed of 5 knots, using the above mentioned filtration coefficient, is 1000 m³ per 3.69 minutes. In this study micronekton standardized volumes, or numbers, per 500 m³ were calculated by the following formula:

$$\text{ml or number}/500\ \text{m}^3 = \frac{\text{actual vol. or number}}{\text{number of minutes}} \times 1.85$$

Brinton (1962) has denoted as plentiful species those which occur in concentrations greater than about 25 specimens per 1000 m³ of water. Of the euphausiid species which mature at $\geqslant 9$ mm, only one, *Euphausia eximia*, was plentiful in the 64-1 and 64-2 collections, and this species was the predominant euphausiid in the samples. For each collection, in the portion of the sample counted, the length of each *E. eximia* was measured to the nearest mm, from the tip of the rostrum to the tip of the telson. In addition to other station data, the percentage of each sample which was counted and measured is noted in Table 1. Excluding station 41, the remainder of each sample was scanned under the microscope for rare species.

DISCUSSION AND SUMMARY

Wilcoxon's signed-rank test (Tate and Clelland, 1957), a nonparametric statistical method, was employed to test for differences in euphausiid catching ability between the two nets. The data in Table 1 indicate that there is no sig-

nificant difference between the nets with respect to estimated volume of total euphausiids per 500 m³. However, it is clear that the nets differ with regard to ability to catch different species and ontogenetic stages. It is evident that the micronekton net does not quantitatively sample larval or juvenile *Euphausia eximia*, and that those animals which are less than 13 mm long escape readily through the larger mesh. In the size range 13–21 mm there appears to be no significant difference in number of *E. eximia* per 500 m³, but there may be such a difference in the 22–28 mm size range; the micronekton net appears to catch more euphausiids in this size range than does the 1-m net. This difference in the 22–28 mm category may be interpreted as evidence of avoidance of the 1-m net by the larger euphausiids. However, when all adults (13–28 mm) are grouped together there is no significant difference between the nets with regard to the estimated density of *E. eximia*. Evidence of avoidance of towed nets by zooplankton has been presented by Fleminger and Clutter (1965).

In terms of the number of euphausiid species found at a station, there was no significant difference between the two nets when adults alone were considered (Table 1). When larvae and juveniles, as well as adults, were used to determine the total number of species present at a station, there was a significant difference between the catches of the two nets. The 1-m net caught more euphausiid species than the micronekton net, because it retained more larvae and juveniles than the micronekton net (Table 1) and also retained more adults of the smaller species (adult at <9 mm in length, Table 2). Table 2 shows a comparison of the two nets with respect to presence or absence of adults of different euphausiid species at nine stations. For the larger species (adult at $\geqslant 9$ mm) the micronekton net as a sampling device is as good as or better than the 1-m net with regard to presence or absence of species (Table 2). Of the smaller species, with the exception of *E. distinguenda* (Table 2), presence of adults was observed more often in the 1-m net than in the micronekton net. Thus, for qualitative euphausiid studies, the 1-m net provides almost as much or more information for one-third of the ship time.

TABLE 1

EUPHAUSIID CATCHING ABILITY OF A MICRONEKTON NET COMPARED WITH A ONE-METER NET

CRUISE AND STA.	POSITION LAT. N. LONG. W.	DATE 1964	NET	LOCAL TIME	DEPTH OF HAUL (M)	MEASURED TOTAL EUPHAUSIID DISPLACEMENT VOLUME, ML PER 500 M³	NUMBER OF SPECIES PRESENT AS LARVAE, JUVENILES, OR ADULTS	AS ADULTS	ESTIMATED NUMBER OF *Euphausia eximia* PER 500 M³ LARVAE 2-4mm	JUVENILES 5-12mm	ADULTS 13-21mm	22-28mm	13-28mm	PERCENT OF SAMPLE COUNTED AND MEASURED
64-1, 23	22° 55' 112° 56'	12 June	Meter	2234-2247	129	4	11	7	4	203	32	6	38	100.00
			Micro-nekton	2251-2350	134	2	10	9	0	<1	11	14	25	25.00
64-1, 29	23° 02' 111° 20'	13 June	Meter	2240-2254	131	<1	8	5	8	20	4	0	4	100.00
			Micro-nekton	2257-2357	135	4	6	5	0	1	26	26	52	25.00
64-2, 03	26° 58' 115° 31'	5 Aug	Meter	2219-2233	134	6	13	6	47	19	7	4	11	100.00
			Micro-nekton	2240-2334	145	5	5	5	0	0	10	29	39	12.50
64-2, 16	25° 33.8''113° 45'	8 Aug	Meter	2239-2253	139	4.5	9	6	31	23	2	15	17	100.00
			Micro-nekton	2258-2352	125	2	5	5	0	0	6	11	17	50.00
64-2, 23	25° 01.7' 113° 23.3'	9 Aug	Meter	2133-2147	134	3.5	9	6	130	1	18	20	38	100.00
			Micro-nekton	2154-2246	140	6	4	4	0	0	10	56	66	12.50
64-2, 29	24° 29.4' 113° 02.1'	11 Aug	Meter	0053-0108	131	3	8	4	15	26	30	8	38	100.00
			Micro-nekton	0114-0210	130	5	4	4	0	0	15	33	48	12.50
64-2, 35	23° 50.7' 112° 42.1'	11 Aug	Meter	2110-2124	136	3	6	4	0	17	10	13	23	100.00
			Micro-nekton	2130-2224	---	6	5	4	0	<1	37	48	85	12.50
64-2, 41	23° 13.5' 112° 18'	13 Aug	Meter	0056-0110	131	39	-	-	16	45	193	251	444	50.00
			Micro-nekton	0116-0212	130	47	-	-	0	0	371	301	672	2.75
64-2, 56	22° 46.3' 110° 22.4'	16 Aug	Meter	0105-0120	134	22.5	6	4	139	798	290	29	319	25.00
			Micro-nekton	0121-0215	128	6	4	4	0	1	52	31	83	12.50
64-2, 58	23° 25' 111°12.5'	16-17 Aug	Meter	2309-2323	126	2	3	1	6	298	12	0	12	100.00
			Micro-nekton	2326-0018	---	3	5	5	0	1	36	14	50	25.00
Wilcoxon's Signed-Rank Test (Tate and Clelland, 1957), T=						20.5	4	6.5	0	0	22	3	11	
						p > .20	p<.05	p >.20	p<.01	p<.01	p>.20	p=.01	p>.20	

TABLE 2

COMPARISON OF THE MICRONEKTON NET AND ONE-METER NET WITH RESPECT TO PRESENCE
OR ABSENCE OF ADULTS OF EUPHAUSIID SPECIES AT NINE STATIONS

| | NUMBER OF STATIONS WHERE ADULTS WERE COLLECTED | | | |
SPECIES	IN METER NET ONLY	IN MICRONEKTON NET ONLY	IN BOTH NETS	IN NEITHER NET
Large species (adult at ≥ 9 mm)				
Euphausia eximia	—	—	9	—
Euphausia gibboides	—	—	5	4
Nematobrachion flexipes	—	5	3	1
Nematoscelis difficilis	—	4	4	1
Nematoscelis gracilis	1	3	—	5
Nyctiphanes simplex	—	2	2	5
Small species (adult at < 9 mm)				
Euphausia diomedeae	1	—	—	8
Euphausia distinguenda	1	3	1	4
Euphausia mutica	1	—	1	7
Euphausia recurva	1	—	1	7
Euphausia tenera	1	—	1	7
Stylocheiron affine	6	—	1	2
Stylocheiron longicorne	2	—	—	7
Thysanoessa gregaria	1	—	—	8

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A New Genus and Two New Species in the Families Volutidae and Turbinellidae (Mollusca: Gastropoda) from the Western Pacific

HARALD A. REHDER[1]

ABSTRACT: *Sigaluta pratasensis,* new genus, new species, in the family Volutidae is described from the South China Sea, off Hong Kong. *Phenacoptygma* Dall, 1918 is removed from the Volutidae and placed in the synonymy of *Surculina* Dall, 1908, which in turn is removed from the Turridae and assigned to the Turbinellidae near *Benthovoluta* Kuroda and Habe, 1950, on the basis of its radula. It is proposed that the families Turbinellidae (*olim* Xancidae) and Vasidae be of coordinate rank. A new species of *Benthovoluta, B. gracilior,* is described from the Sulu Sea, Philippines.

IN THE PROCESS of arranging the specimens of the family Volutidae in the Division of Mollusks, U. S. National Museum, two new species of deepwater mollusks from the western Pacific were found. These were dredged by the U. S. Bureau of Fisheries steamer "Albatross I" in the South China and Sulu Seas during her 1907–09 cruise in the Philippine Islands.

One of these species turns out to belong to the genus *Benthovoluta,* recently placed by Kuroda (1965:50–51) in the family Turbinellidae. For the other a new genus in the family Volutidae must be erected.

VOLUTIDAE

Sigaluta,[2] new genus

Shell moderately large, ovate with only few whorls (about 4); nuclear whorls large; shiny with glazelike surface. Aperture ovate; outer lip slightly flaring and somewhat thickened, with shallow rounded sinus at junction with body whorl; columella straight, bearing 2 strongly ascending spiral folds.

TYPE SPECIES: *Sigaluta pratasensis,* new species

This interesting new genus is represented in our collection by only two shells, and as the

soft parts unfortunately were not retained, the exact allocation of the genus must await the discovery of fresh living material. On the basis of the general appearance of the shell, nucleus, and columella plaits, I am placing this genus temporarily in the subfamily Cymbiinae, tribe Meloides, as defined by Pilsbry and Olsson (1954:16–17).

Sigaluta pratasensis, new species
Figs. 1–4

DESCRIPTION: Shell of moderate size (54–61 mm, 2¼–2½ inches long) and solidity, narrowly ovate; nuclear whorls 2¼, large, bulbous, smooth, shining; transition between nuclear and postnuclear whorls marked by faint line of demarcation and slight increase in diameter of first postnuclear whorl; postnuclear whorls 1¾–2, smooth and shining as if glazed; body whorl rather strongly descending on penultimate whorl; suture glazed over; outer lip slightly thickened with a whitish callus and marked with a shallow sigmoid sinus below suture and a broad, very shallow sinus at obliquely truncate base. Aperture narrowly ovate, acuminate at top, broadly truncate at base; columella straight, bearing 2 strongly ascending spiral plaits. Color from light yellow-brown (#76) (with a slightly grayish cast) to light-gray olive-brown (#94) (ISCC-NBS Color Names, Kelly and Judd, 1965).

LOCALITY: West of Pratas Reef, South China Sea, in 208 fathoms (380 m); U.S.B.F. "Alba-

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[2] From the Greek *sigaleios* (glossy) + *Voluta.*

tross I" Sta. 5301, 20° 37′ N, 115° 43′ E, gray mud and sand bottom. August 8, 1908.

MEASUREMENTS:

SPECIMEN	LENGTH	WIDTH
Holotype (USNM 237018)	53.9 mm	28.5 mm
Paratype (USNM 637251)	60.95 mm	29.6 mm

TURBINELLIDAE Swainson, 1840

SYNONYMS: Ptychatractidae Stimpson, 1865; Xancidae Woodring, 1928

Benthovoluta Kuroda and Habe, 1950

Kuroda, T. and T. Habe, 1950:37.
Kuroda, T., 1965:50–52.

FIGS. 1 and 2. *Sigaluta pratasensis* n. gen., n. sp.; approx. × ⅘. *1*, Paratype. *2*, Holotype.

TYPE SPECIES, BY ORIGINAL DESIGNATION: *Phenacoptygma? kiiensis* Kuroda (=*Voluta hilgendorfi* von Martens, 1897).

Kuroda (1931:48) described the type species, under the name *Phenacoptygma kiiensis,* locating it doubtfully in that eastern Pacific genus and suggesting that *"Mitra" plicifera* Yokoyama (Yokoyama, 1920:48) from a Pliocene formation near Tokyo Bay was related. In 1950 Kuroda and Habe, in proposing the new genus *Benthovoluta,* placed *kiiensis* Kuroda in the synonymy of *Voluta hilgendorfi* von Martens, although designating *P. kiiensis* as the type species of the genus. At the same time they listed *"Mitra" plicifera* Yokoyama as an additional synonym of *hilgendorfi.* Judging from the figure and description of the Pliocene *plicifera,* I would suggest that it represents a distinct species, with more numerous axial ribs on the spire whorls, which are less convex than in *hilgendorfi.*

The species described below seems to represent a third species of this genus, although without a knowledge of its soft parts its allocation to this group must be largely speculative.

Habe (1952:132) depicted the radulae of a number of Japanese marine mollusks without comments. Among them was a figure of the teeth of *Benthovoluta hilgendorfi.* Kuroda (1965:50–51) called attention to the fact that Habe's figure is unlike that of any volutid radula and suggested that *Benthovoluta* be placed in the family Turbinellidae, near *Metzgeria* Norman, 1879, a monotypic boreal genus. A comparison of Sars' figure (Sars, 1878, pl.

FIG. 3. *Sigaluta pratasensis* n. gen., n. sp.; apical view; approx. × ⅘.

FIG. 4. *Sigaluta pratasensis* n. gen., n. sp.; view showing columella fold; approx. × ⅘.

IX, fig. 13; Thiele, 1929:343, fig. 409) of the radula of *Metzgeria alba* (Jeffreys, 1873) (syn. *Meyeria pusilla* 'M. Sars' G. O. Sars, 1878) with the figure given by Habe reveals indeed a very close similarity; while the radulae of *Turbinella fusus* Sowerby, 1825, as published by Dall (1885:346, pl. XIX, fig. 1; Abbott, 1950:202, pl. 89, fig. 2) and of *T. laevigata* Anton, 1839 (Thiele, 1929:342; Abbott, 1950: 202, pl. 89, fig. 3) also show a similarity, although the relationship is less close.

A more strikingly close relationship is revealed by a study of the radulae of what Dall described as *Daphnella* (*Surculina*) *cortezi* (Dall, 1908:292) from off San Diego, California, and *?Leucosyrinx galapagana* (Dall, 1919:5, pl. 3, fig. 2) from the Galapagos Islands. The type species of *Surculina, Daphnella* (*Surculina*) *blanda* Dall (1908:291, pl. 3, fig. 1) is certainly congeneric with *S. cortezi,* for which Dall in 1918 proposed the generic name *Phenacoptygma* (Dall, 1918:138), placing it in the family Volutidae. This genus was placed in the subfamily Calliotectinae by Pilsbry and Olsson (1954:19).

The genus *Surculina* Dall, 1908 (Dall, 1908:260–261), with its synonym *Phenacoptygma* Dall, 1918, therefore also must be placed in the family Turbinellidae.

Surculina was considered to be a subgenus of *Leucosyrinx* by Grant and Gale (1931:509–510), who assigned both *blanda* and *galapagana* to this subgenus. Powell (1942:21) follows this allocation, placing the group in the subfamily Cochlespirinae.

In order to make this relationship more clear, and because the type species of *Surculina* apparently has never been figured and the figures of the other species may not be readily accessible to all students, I am illustrating all three species of *Surculina* (Figs. 7–9). In addition, I am figuring the radula of *S. cortezi* (Fig. 10) and, for comparison, that of *Benthovoluta hilgendorfi* (Fig. 11).

Another genus that probably belongs here is *Ptychatractus* Stimpson (1865:59) with three species: the type of the genus, *P. ligatus* Mighels and Adams, 1842, from the Gulf of Maine; *P. occidentalis* Stearns, 1873, from Alaska; *P. californicus* Dall, 1908, from Monterey Bay to San Diego, California. A rather poor figure of the radula is given by Stimpson (1865: pl. 8, fig. 8).

I have used the family name Turbinellidae instead of Xancidae or Vasidae for the following reason.

In 1957, in Opinion 489 of the International Commission on Zoological Nomenclature, the generic name *Turbinella* Lamarck, 1799 was validated and placed on the Official List of Generic Names, and *Xancus* Röding, 1798 was suppressed and placed on the Official Index of Rejected and Invalid Names. Concurrently, the family name Turbinellidae Swainson, 1840 was placed on the Official List of Family Group Names in Zoology. A perusal of the history of this case (Hemming, 1957:155–178) reveals the fact that whereas six persons are cited as supporting the use of *Turbinella,* eight opposed it. Of these eight, six were professional malacologists (one a paleontologist), while three malacologists (only one of them a professional worker) supported the proposal, siding with a botanist, an ichthyologist, and an anthropologist.

In spite of the preponderance of opposition against the proposal, and the clear evidence of the very limited use of *Turbinella* in recent scientific literature, the proposal was approved and Opinion 489 was issued as summarized above.

Disturbed by the action of the International Commission in passing a ruling so contrary to the majority of considered opinion, many malacologists have refused to follow the recommendation, and have continued to use *Xancus* and Xancidae, apparently hoping for an eventual reversal of this Opinion. This procedure, however, appears to me to be unwise. If we wish to have any kind of stability in nomenclature, and if the decisions of the International Commission on Zoological Nomenclature are to have any meaning, we must accept the final decisions of the Commission, particularly as regards names placed on the official lists. What scientific workers must do in the future is to act promptly to prevent decisions by the International Commission on Zoological Nomenclature that are contrary to the evidence and majority opinion.

In his monograph of several genera of the family Vasidae in the Indo-Pacific, Abbott

(1959:15) proposed to divide the family into two subfamilies, Vasinae and Xancinae, on the basis of differences in the radula and shell characters. On the basis of the rather fundamental differences in the radula, and in order to minimize to some extent the disturbance to nomenclature caused by the action described above, I suggest that these subfamilies be raised to the rank of families. In this way we can retain the well-known family name Vasidae H. and A. Adams, 1853.

Benthovoluta gracilior, new species
Figs. 5 and 6

DESCRIPTION: Shell of moderate size (50–60 mm, about 2 inches long), fusiform, white, with a thin, light or straw yellow periostracum which under the microscope is seen to be minutely rough and lamellately scabrous, especially in the area between suture and peripheral angulation of the ribs. Nuclear whorls $1\frac{1}{4}$, smooth, bulbous; postnuclear whorls about $10\frac{3}{4}$ in holotype and largest paratype; first 5 whorls show about 8 strong ribs, markedly angulate at the periphery and crossed by 3 or 4 spiral cords below the periphery; area above the periphery smooth in earliest whorls, but showing spiral threads that gradually increase in strength; later whorls with more ribs (13–14 in penultimate whorl), which are less strongly angulated, and with fine spiral cords over the entire surface; last

FIG. 7. *Surculina blanda* (Dall, 1908). Holotype; × 2.

FIG. 8. *Surculina cortezi* (Dall, 1908). Holotype; × 1.

FIGS. 5 and 6. *Benthovoluta gracilior* n. sp.; approx. × 1. 5, Paratype. 6, Holotype.

FIG. 9. *Surculina galapagana* (Dall, 1919). Holotype; × 3.
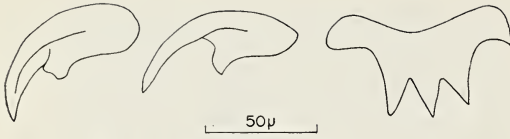
FIG. 10.   Radula teeth of *Surculina cortezi* Dall, showing two views of the lateral and the rachidian.
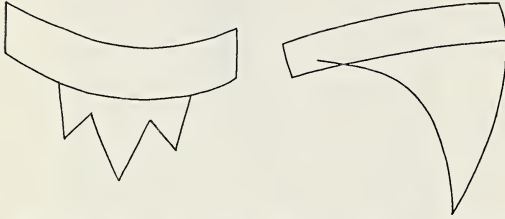
FIG. 11.   Radula teeth of *Benthovoluta hilgendorfi* (von Martens, 1897). Copied from Habe, 1952.

whorl considerably longer than spire, with a long, straight, open anterior canal; outer lip broken in all specimens, but apparently simple, thin; columella with 2 low spiral folds, the upper fold larger.

LOCALITY: Off Cagayan Islands, northern Sulu Sea, Philippines, in 508 fathoms; U.S.B.F. "Albatross I" Sta. 5423, 9° 38′ 30″ N, 121° 11′ E, gray mud and coral sand bottom; March 31, 1909. Six specimens collected.

MEASUREMENTS:

SPECIMEN	LENGTH	WIDTH
Holotype (USNM 637252)	54.75 mm	13.4 mm
Figured Paratype (USNM 238408)	57.75 mm	12.9 mm

REMARKS: This species differs from both *B. hilgendorfi* von Martens and *B. plicifera* Yokoyama in being more slender, with a thinner shell, and with the axial ribs more angulated at the periphery.

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Pogonophora from the Northeastern Pacific: First Records from the Gulf of Tehuantepec, Mexico

Oluwafeyisola S. Adegoke[1]

Northeastern Pacific records of species of the Phylum Pogonophora Johansson, 1937 are few. In all, eight species have been recorded. The first was by Kirkegaard (1956a, 1961) who described *Lamellisabella ivanovi* from the Gulf of Panama. In two successive records, Ivanov (1961, 1962) described *Galathealinum brachiosum,* and *Heptabrachia ctenophora* and *H. canadensis,* respectively, from the west coasts of Canada and Oregon. Hartman (1961) recorded abundant occurrences of *Siboglinum veleronis* Hartman from the La Jolla Canyon off the coast of southern California. Southward (1962) next described *Galathealinum arcticum* from Arctic waters off the northern coast of Yukon, Alaska; and more recently, Cutler (1965) described two new species of *Siboglinum, S. albatrossianum* and *S. ecuadoricum,* and an undetermined specimen, from collections dredged off Cape San Francisco, Ecuador, by the U. S. Fish Commission steamer "Albatross" in 1888.

The occurrences of a few dark-brown, cylindrical collar segments, measuring about 2.9–4.0 mm across, and 3.3 mm long, from West Cortes, East Cortes, and Long Basins, and from the San Diego Trench, were recorded by Hartman and Barnard (1960). These were later referred to the genus *Galathealinum* Kirkegaard, 1956 by Hartman (1961:546), who also mentioned a new record of another species of *Siboglinum* closely resembling *S. veleronis* from "Velero IV" Station 7231, off San Eugenio Point, Lower California, Mexico.

ACKNOWLEDGMENTS

MATERIAL STUDIED

The new species, *Galathealinum mexicanum* sp. nov., described below is the fourth species to be described in the genus *Galathealinum.* It was dredged by the Vermillion Sea Expedition (1958) from a depth of 3531–3603 m in the Gulf of Tehuantepec, Mexico (Univ. Calif. Mus. Paleo. locality B-7469). It is the first pogonophoran record from the Gulf of Tehuantepec.

Only the dried remains of the tubes are preserved. These dark brown tubes are thick-walled and rigid, and have preserved their true cylindrical shape. They taper slightly and uniformly, have an average diameter of over 2.0 mm, and are prominently subdivided along the entire length into segments, each about twice as long as the average diameter of the tube. The exterior of the tubes is covered by a thin, feltlike layer composed of fine and coarse fibers. The coarse fibers are more prominent and more numerous near segmental junctions. These characters place this species within the genus *Galathealinum* as defined by Kirkegaard (1956) and Ivanov (1963).

Although most Recent pogonophoran genera and species are established primarily on the

basis of soft part anatomy, remains of well-preserved tubes are also known to be sufficiently reliable for "specific diagnosis" (see Hartman, 1961:546; Ivanov, 1963:120). The latter author firmly established the validity of this contention by constructing a dichotomous key for the identification of most Recent pogono-phoran species from remains of their tubes (Ivanov, 1963:456–461). The characters of the tubes described and figured in this report readily distinguish them from the three previously described species of *Galathealinum*. It is hoped that, in the future, preserved material from the same area will provide data on the nature of the soft part anatomy of the new species.

SYSTEMATIC DESCRIPTION

Phylum POGONOPHORA Johansson, 1937
    Order THECANEPHRIA Ivanov, 1955
    Family POLYBRACHIIDAE Ivanov, 1952
    Genus *Galathealinum* Kirkegaard, 1956

Galathealinum Kirkegaard, 1956, Galathea Rept. 2:79–83.

TYPE SPECIES: *Galathealinum bruuni* Kirkegaard.

Galathealinum mexicanum sp. nov.

Figs. 1–7

DIAGNOSIS: *Galathealinum* with elongate, cylindrical, segmented tube; circular cross-sectional outline; average tube diameter 2.0–2.5 mm; covered along entire length by thin, felt-like layer of fine and coarse fibers; individual coarse fibers at segmental junction about 15–22μ thick; segment length approximately twice the diameter.

DESCRIPTION: This species is represented by fragments of dried tubes only. The tubes are brownish-gray to dark-gray, elongate and slender. The longest fragment (holotype, Fig. 1) is 147.5 mm long. Maximum diameter 2.5 mm, minimum diameter 1.96 mm. Externally, the tube is divided into numerous prominent segments (see Figs. 1–6). These segments have a circular cross-sectional outline and are of rather uniform length, each measuring 3.8–4.9 mm. The widened funnel-like frills that are prominently shown at the nodes of the described
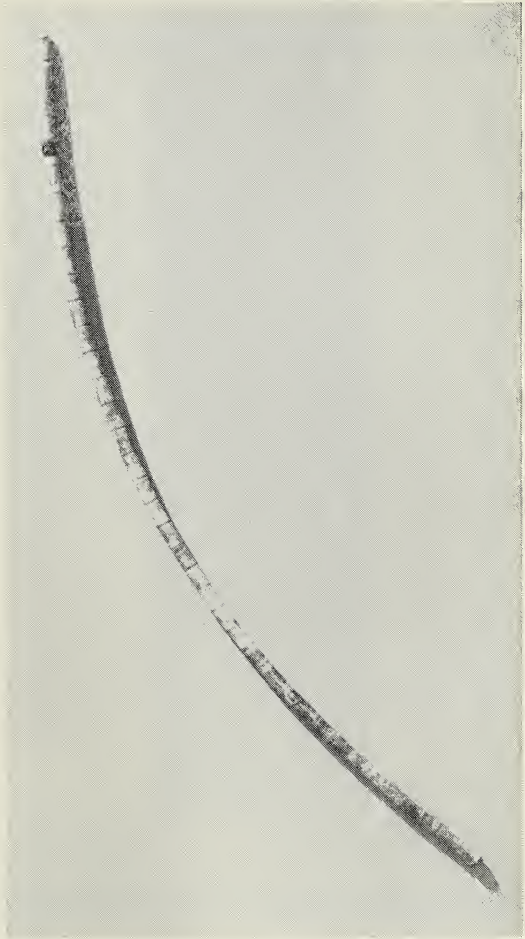
FIG. 1. *Galathealinum mexicanum* Adegoke sp. nov. Tubes from Univ. Calif. Mus. Paleo. locality B-7469, Gulf of Tehuantepec, Mexico. Holotype, UCMP 32882. Entire specimen showing long, curved, segmented tube, × ¾.

species of *Galathealinum* are only poorly preserved on the dried tubes of the present species (Figs. 3, 7). The coarse fibers generally associated with these frills are well developed, however, and are more abundant at the nodes than in the much longer internodes. The exterior of the tube is coated by a thin, friable, feltlike layer, mostly composed of numerous, very fine, light-brown fibers, and few, coarse, reddish-brown, glistening fibers. The latter also penetrate the tube wall and appear as faint ridges on the otherwise smooth interior surface. About 60–80 coarse fibers are present in each internode. Though essentially transverse, they are

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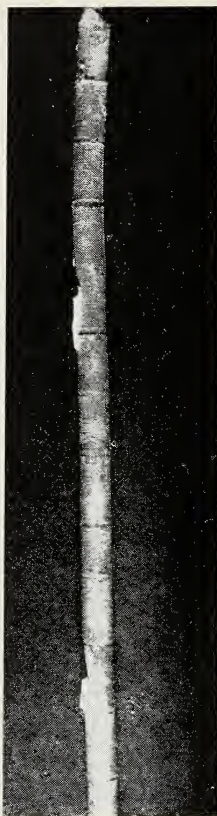
FIG. 2. *Galathealinum mexicanum* Adegoke sp.
nov. Paratype, UCMP 12155. Anterior region of para-
type showing well-defined segments, coarse transverse
fibers, and some encrusting calcareous annelid tubes,
× 1.7.

FIG. 3. *Galathealinum mexicanum* Adegoke sp.
nov. Anterior end of holotype showing a few seg-
ments with coarse fibers and remnants of segmental
frills at the nodes, × 5.

FIG. 4. *Galathealinum mexicanum* Adegoke sp.
nov. Part of holotype enlarged to show irregular
coarse fibers, × 5.

rather irregularly oriented, and a few are even
confluent. The interior wall is a glossy, dark-
brown color, and is devoid of the feltlike layer.
Both the extreme anterior and posterior ends of
the tubes are unknown.

DIMENSIONS: Holotype: length 147.5 mm, di-
ameter of wider anterior end 2.5 mm, diameter
of smaller posterior end 2.2 mm, average length
of segments 4.0 mm, thickness of wall 0.1 mm,
thickness of coarse fibers 15–22μ. Paratype:
length 77.5 mm, diameter of wider anterior end
2.4 mm, diameter of posterior end 1.96 mm,
average length of segments 4.5 mm, thickness
of wall about 0.1 mm, thickness of coarse fibers
15–22μ.

HOLOTYPE: Univ. Calif. Mus. Paleo, no.
32882, locality B-7469.

PARATYPE: UCMP no. 12155, from type local-
ity.

OCCURRENCE: UCMP locality B-7469. Few
tubes and some echinoids dredged by the Ver-
million Sea Expedition S.I.O., from the Gulf
of Tehuantepec, Mexico. Latitude 14°28′N to
14° 29′N. Longitude 93° 09′W to 93° 10′W.
Depth 1,935–1,974 fathoms. Field no. P-128-
58.

REMARKS: *Galathealinum mexicanum* sp.
nov. resembles other described species of *Gala-
thealinum* in the possession of a dark-brown,
segmented tube covered externally by a thin, fri-
able, feltlike layer. Its dimensions are closest to
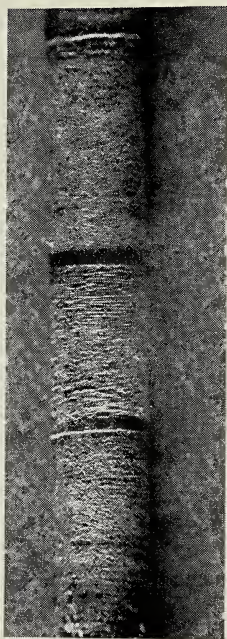
FIG. 5. *Galathealinum mexicanum* Adegoke sp. nov. Part of paratype enlarged to show coarse fibers and details of constricted segmental junctions, × 5.
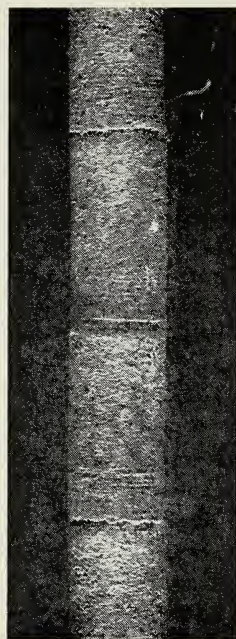
FIG. 7. *Galathealinum mexicanum* Adegoke sp. nov. Part of paratype enlarged to show details of segmental junction and remnants of segmental frills at nodes.
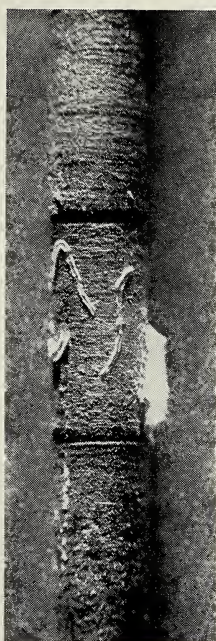
FIG. 6. *Galathealinum mexicanum* Adegoke sp. nov. Part of paratype enlarged to show three encrusting annelid tubes, × 5.

those of *G. brachiosum* Ivanov, whose diameter ranges from 2.0 to 2.6 mm, from which it may be readily distinguished by the longer segments (about 4.0 mm long as against 1 mm in *G. brachiosum*; see Ivanov, 1963: Fig. E162). Moreover, the coarse fibers in the new species measure 15–22µ, whereas they are 7–12µ thick in *G. brachiosum*.

From *G. bruuni* Kirkegaard, the new species may be distinguished by its larger dimensions, relatively weaker segmental frills, and thicker, coarser fibers (2–4µ thick in *G. brunni*).

The new species may be readily distinguished from *G. arcticum* Southward by its larger diameter (1.33–1.95 mm in the latter); larger length-diameter ratio of each segment, which is about 2 in the new species and 1 in *G. arcticum*; and the thicker coarse fibers, which are only 1–2µ thick in *G. arcticum*.

The longest fragment represented in the collection is 147.5 mm long. As the extreme anterior and posterior ends of this tube are not represented, and because of the rather minor variation in taper between the two ends (anterior diameter 2.5 mm, posterior diameter 2.2

mm), it is here suggested that the total actual
length of the tube may be several times the
length of this fragment.

Segmental funnel-like frills, a common char-
acteristic of the genus, are only weakly repre-
sented here (Figs. 3, 7). According to Ivanov
(1963:412), these frills are soft and pliant in
G. brachiosum and consist entirely of the exter-
nal fibrous layer. It is, therefore, easily conceiv-
able that these frills, originally present on this
new species, became shrunken and inconspic-
uous because of the poor conditions of preserva-
tion of the tubes. The marked concentration of
irregularly oriented coarse fibers in the vicinity
of each segmental junction (see Figs. 3, 4) sup-
ports this contention.

Pogonophoran tubes are generally straight.
Most of the tubes of this species in the collec-
tion studied are also straight (see Fig. 2). A
few, however, are curved (see holotype, Fig.
1). This curvature is considered to be a shrink-
age phenomenon, as a result of drying.

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Studies in the Calcium and Phosphorus Metabolism of the Crab, *Podophthalmus vigil* (Fabricius)[1]

Bryant T. Sather[2]

ABSTRACT: By employing modifications of the molt classification by Drach (1939) and Hiatt (1948), it was discovered in laboratory-maintained crabs (*Podophthalmus vigil*) that a partial desiccation occurred during proecdysis followed by a rehydration at the A stages.

The inorganic and organic content of the carapace, mid-gut gland, gills, and muscles were followed during the molt cycle. The carapace had the greatest inorganic fluctuations. The mid-gut gland and muscle tended to increase in both organic and inorganic matter during premolt, suggesting that these organs may serve as reservoirs for these components.

The calcium and total phosphorus constituents of these organs and of the blood were determined at the various molt stages. Fluctuations in the amounts of these two elements were observed in all sampled tissues. The storage of calcium in the mid-gut gland and muscles during premolt is discussed. Phosphorus was found to be stored in the digestive gland during postecdysis but not in proecdysis. The muscle also tended to store phosphorus during premolt.

As *P. vigil* becomes older, i.e., larger, it is unable to resorb from the exoskeleton the same quantity of calcium, but it is able to recalcify the new exoskeleton to the same extent as does a smaller crab.

CALCIFICATION and hard tissue formation occurs in many forms of life. It is found in bacteria (Ennever, 1963; Rizzo, et al., 1963; Greenfield, 1963), algae (e.g., *Porolithon* and *Halamita*), protozoans (Isenberg, et al., 1963; Bé and Ericson, 1963), coelenterates, echinoderms, molluscs, arthropods, and vertebrates. Generally, the function of calcification is to give form, support, and protection, and to contribute in ionic homeostasis (Urist, 1962), but in some instances calcification can be considered a pathological condition. The calcium complex deposited may be in three forms—calcite, aragonite, and apatite. The latter is a calcium phosphate $[Ca_{10}(PO_4)_6(OH)_2]$ and the others are calcium carbonate complexes. Very little phosphorus is found in calcite and aragonite, which are generally restricted to the lower phyla. The amount of strontium and magnesium, the crystal structure, and the density of the calcium carbonate determine the difference between aragonite and calcite. The latter has little strontium and magnesium present in its hexagonal, less dense crystalline structure. Apatite is found in vertebrate bone, dentine, cementum, and enamel. Regardless of the crystal structure and the phylogenetic group in which it occurs, the process of calcification can be considered to be basically the same (Travis, 1960, 1963), although the function may be specifically adapted for different requirements.

In crustaceans, molting is necessary in the apparent growth process. Thus, considerable quantities of calcium and organic constituents have to be resorbed from the exoskeleton prior to ecdysis, but total resorption is limited to certain areas, i.e., the endophragmal skeleton and the ecdysial sutures. After resorption (via the blood) of these constituents, the organism is confronted with an abnormally high concentration of these substances in its internal fluids and the animal must either store or excrete this

excess. If the availability of the resorbed constituent is sparse, the majority of this element is usually stored. Crayfish generally store some of the resorbed calcium and phosphorus as small buttons, called gastroliths, in the lining of the stomach. Gastrolith formation and dissolution have been followed throughout the ecdysis cycle by Damboviceanu (1932), Numanoi (1937), Keyer (1942), Scudamore (1942, 1947), Travis (1955b, 1960, 1963), and McWhinnie (1962). Marine crustaceans generally store some of the resorbed calcium and phosphorus in the mid-gut gland. Paul and Sharpe (1916) have reported that this process occurs in *Cancer pagurus*. This also occurs in *Carcinus maenas* (von Schönborn, 1912; Robertson, 1937), in *Maia squinado* (Drach, 1939), in *Hemigrapsus nudis* (Kincaid and Scheer, 1952) and in the lobster, *Panulirus argus* (Travis, 1955a). Miyawaki and Sasaki (1961) found the same in the fresh water crayfish, *Procambarus*. Calcium is present in relatively high concentrations in sea water and therefore this element may not be a limiting factor in molting, and so not much of it may need to be stored during proecdysis of a marine crab. The concentration of phosphate in Hawaiian waters, however, is small (Sather, 1966), and therefore it would seem to be necessary for the animal to conserve this element to a greater extent than calcium. After ecdysis is completed, the organism would use the resorbed and stored materials for calcification of the new exoskeleton. The amount of inorganic material stored, however, is not sufficient to account for the total amount found in the intermolt crustacean. Therefore, the animal must actively concentrate the elements from the environment.

The molt cycle of crustaceans has been the subject of a great number of investigations. Apart from descriptions of morphological changes, the mineral metabolism has been studied to a certain extent, particularly changes in calcium and phosphorus content (Travis, 1954, 1955b, 1963). But such changes have been investigated only at random periods in the molt cycle, and only in certain tissues and organs (glands). Some emphasis has been placed on the effect of hormonal influences (eyestalk hormones, etc.) on the alterations (Carlisle, 1954; McWhinney, 1962). No data have been avail-

able on calcium and phosphorus metabolism throughout the entire molt cycle of a crab, nor has anything been known of the concentrations and distribution of these elements in the animal at times of calcification and decalcification, periods of major importance in the cycle. Therefore, these studies were undertaken on the physiological processes which occur in the molt cycle of the crab, *Podophthalmus vigil*.

MATERIALS AND METHODS

In the period from March 1961 to October 1963, approximately 1,450 specimens of *P. vigil* were collected from Kaneohe Bay, Oahu, Hawaii and transported to the University of Hawaii Marine Laboratory. The animals were sexed, staged, tagged, and placed in aquaria with a continuous supply of fresh sea water. Modifications of the classification schemes of Drach (1939) and Hiatt (1948) were employed to determine the molt stages of *P. vigil*. A descriptive analysis of the molt scheme was presented by Sather (1966). Crabs in the same stage were placed in a specific aquarium. The animals were usually fed pieces of frozen fish twice a week, but occasionally fresh crab muscle or frozen beef liver was substituted.

When a crab reached a desired stage, it was removed from the aquarium and carefully dried with tissue paper. A 1 ml blood sample was taken from the heart by making a small hole with a dental drill in the carapace immediately posterior of the cardiac and mesobranchial suture and inserting a No. 21-gauge hypodermic needle fitted to a syringe into the exposed pericardium. The crab was then killed and rinsed with distilled water. The gills, mid-gut gland, muscle, and carapace were dissected free, and these, together with the "remainder," were placed into separate tared crucibles. After weighing, the crucibles were placed in a drying oven for 12 hours at 114°C. After weighing, they were dry-ashed at 550°C for 24 hours. The fresh, dry, and ashed weights were recorded and the water, organic, and inorganic contents were calculated. Aliquots of the ashed tissues were taken for the determinations of calcium and phosphorus. The blood samples were stored for later chemical analysis. The exuviae were treated in the same manner except that the fresh

weights were not determined because it was not possible to dry thoroughly the gills and endophragmal skeleton.

The flame spectrophotometric analysis of Geyer and Bowie (1961) was used to determine the calcium content of the ashed samples. The blood calcium was determined using the method of Ferro and Ham (1957a, 1957b). The method of Bernhardt, Chess, and Roy (1961) was used to determine the phosphorus (P_2O_5) content in both the ashed and blood samples. All flame spectrophotometric determinations were carried out on a Beckman DU spectrophotometer equipped with a hydrogen-oxygen burner and a photomultiplier. Blank samples were carried throughout the analysis.

The hydration, organic, inorganic, calcium, and phosphorus data were transformed to arcsin values and the latter were statistically analyzed to determine whether interactions between the various parameters were present. The parameters were also subjected to the D-test of Hartley to ascertain the differences among the means (Snedecor, 1959).

RESULTS

Table 1 contains the results of the statistical interaction analysis. The law of probability values indicate that interactions of hydration, organic, inorganic, calcium, and phosphorus contents had occurred, which illustrates that the chemical parameters of the organs did not uniformly fluctuate from one molt stage to another. The interactions demonstrate that the components were being accumulated by the various

organs during different stages, which suggests that the constituents were being transferred between organs at different times.

The results of the statistical comparisons of per cent hydration, inorganic and organic, and calcium and phosphorus among the means are incorporated in Tables 2, 3, and 4, respectively. The concentrations of the components in the various organs, throughout the molt cycle, are listed in decreasing order. In Table 2 the appearance of a superscript number in a molt period signifies that the content of the organ at that period is greater than those with a lesser superscript and without a superscript. The contents during molt periods having equal superscripts are not statistically different from each other. For example, the hydration of the mid-gut gland (Table 2) during the C_{3-4} period is significantly greater than that during C_{1-2}, B_{1-2}, A_{1-2}, D_{1-2}, and D_{3-4}. The amounts of mid-gut gland water during the C_{1-2}, B_{1-2}, and A_{1-2} periods are greater than those during D_{1-2} and D_{3-4}; but, the amounts at the C_{1-2}, B_{1-2}, and A_{1-2} periods do not significantly differ from each other.

The ordinates of Figures 1–7 are expressed as per cent content, which is not the most ideal

TABLE 1

INTERACTION ANALYSIS OF PERCENTAGE, COMPOSITION OF FIVE COMPONENTS IN SAMPLED ORGANS OF *P. vigil*

% COMPOSITION	no	F-VALUE	PROBABILITY
Hydration+	16.36	55.33	< 0.01
Organic	15.78	7.56	< 0.01
Inorganic	15.98	27.86	< 0.01
Calcium	15.04	2.86	< 0.01
Phosphorus	11.30	5.86	< 0.01

no = average number in each class.
+ = calculated real values.
f_1, f_2 (degrees of freedom) = 20 and 400, respectively.

TABLE 2

COMPARISON AMONG THE MEANS: PER CENT HYDRATION OF FOUR ORGANS OF *P. vigil* THROUGHOUT THE MOLT CYCLE

ORGAN AND CONCENTRATION IN DECREASING ORDER

CARAPACE	GILL	MID-GUT GLAND	MUSCLE
A_{1-2}^{5}*	C_{1-2}^{3}	C_{3-4}^{5}	C_{3-4}^{4}
B_{1-2}^{4}	C_{3-4}^{3}	C_{1-2}^{2}	C_{1-2}^{4}
C_{3-4}	B_{1-2}^{3}	B_{1-2}^{2}	B_{1-2}^{2}
C_{1-2}	A_{1-2}^{1}	A_{1-2}^{2}	A_{1-2}^{2}
D_{3-4}	D_{1-2}	D_{1-2}	D_{3-4}
D_{1-2}	D_{3-4}	D_{3-4}	D_{1-2}

* Explanation of superscript numbers:
5 = Significantly greater content than those in the last 5 stages.
4 = Significantly greater content than those in the last 4 stages.
3 = Significantly greater content than those in the last 3 stages.
2 = Significantly greater content than those in the last 2 stages.
1 = Significantly greater content than those in nonsuperscripted stages.

TABLE 3

Comparison Among the Means: Organic and Inorganic Contents of Four Organs of *P. vigil* Throughout the Molt Cycle

ORGAN AND CONCENTRATION IN DECREASING ORDER

CARAPACE	GILL	MID-GUT GLAND	MUSCLE
% ORGANIC			
D_{3-4}	D_{3-4}[3*]	D_{1-2}[4]	D_{1-2}[4]
C_{1-2}	A_{1-2}[3]	D_{3-4}[4]	D_{3-4}[4]
C_{3-4}	D_{1-2}[3]	A_{1-2}[1]	A_{1-2}[2]
B_{1-2}	B_{1-2}	C_{1-2}[1]	B_{1-2}[2]
A_{1-2}	C_{1-2}	B_{1-2}[1]	C_{1-2}
D_{1-2}	C_{3-4}	C_{3-4}	C_{3-4}
% INORGANIC			
D_{1-2}[5]	D_{1-2}[4]	D_{3-4}[5]	C_{3-4}
D_{3-4}[2]	D_{3-4}	D_{1-2}[2]	D_{1-2}
C_{3-4}[2]	C_{3-4}	A_{1-2}[1]	C_{1-2}
C_{1-2}[2]	C_{1-2}	B_{1-2}[1]	D_{3-4}
B_{1-2}[1]	B_{1-2}	C_{3-4}	B_{1-2}
A_{1-2}	A_{1-2}	C_{1-2}	A_{1-2}

* For explanation of superscript numbers see legend for Table 2.

TABLE 4

Comparison Among the Means: Calcium and Phosphorus Contents of Five Organs Throughout the Molt Cycle

ORGAN AND CONCENTRATION IN DECREASING ORDER

CARAPACE	GILL	MID-GUT GLAND	MUSCLE	BLOOD
% CALCIUM				
C_{3-4}[2*]	C_{3-4}[1]	D_{3-4}[1]	D_{3-4}[1]	D_{1-2}[5]
D_{3-4}[2]	D_{3-4}[1]	D_{1-2}[1]	C_{3-4}	B_{1-2}
D_{1-2}[1]	C_{1-2}[1]	C_{3-4}	D_{1-2}	C_{1-2}
C_{1-2}[1]	A_{1-2}[1]	A_{1-2}	C_{1-2}	C_{3-4}
B_{1-2}	D_{1-2}[1]	B_{1-2}	A_{1-2}	A_{1-2}
A_{1-2}	B_{1-2}	C_{1-2}	B_{1-2}	D_{3-4}
% PHOSPHORUS				
A_{1-2}[5]	D_{3-4}	B_{1-2}[1]	D_{1-2}[1]	D_{1-2}[4]
B_{1-2}[2]	C_{3-4}	C_{1-2}[1]	A_{1-2}[1]	D_{3-4}[1]
C_{1-2}[1]	C_{1-2}	A_{1-2}[1]	C_{1-2}	C_{1-2}
D_{3-4}	B_{1-2}	C_{3-4}[1]	B_{1-2}	A_{1-2}
C_{3-4}	A_{1-2}	D_{1-2}[1]	D_{3-4}	B_{1-2}
D_{1-2}	D_{1-2}	D_{3-4}	C_{3-4}	C_{3-4}

* For explanation of superscript numbers see legend for Table 2.
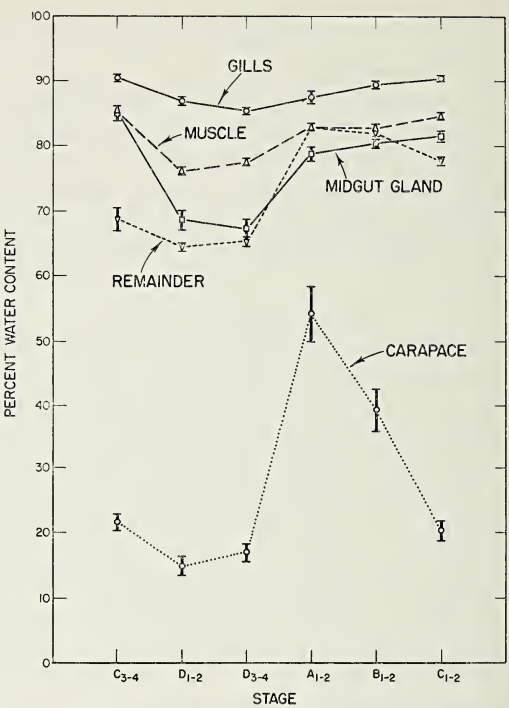
FIG. 1. Changes (mean ± S.E.) in the water content of five organs of *P. vigil* during the molt cycle.

index. Alterations in one component, e.g., organic content, may affect the per cent composition of another component, i.e., inorganic content. Therefore, losses or gains in one particular constituent may only reflect losses or gains in another. Alterations in per cent composition were chosen because the data appearing in most of the literature were expressed in these terms and, thus, this index made comparisons more accessible.

More expressive indices would be: mg or mEq/mg N, or mg or mEq/gm water. The latter ratio is more valid when comparisons of equilibria are desired (Robertson, 1960).

Figure 1 illustrates the alterations in water content of the carapace, mid-gut gland, muscle, gills, and "remainder" during the molt cycle. It is clear that the organs become somewhat dehydrated during proecdysis and rapidly rehydrated during ecdysis.

The organic and inorganic contents of the four organs are plotted in Figures 2 and 3, respectively. The comparable data for the "remainder" were not determined because this por-
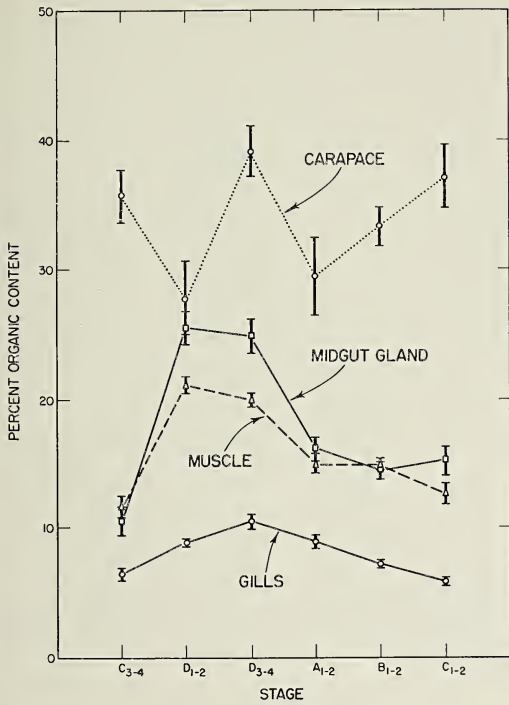
FIG. 2. Changes (mean ± S.E.) in the organic content of four tissues of *P. vigil* during the molt cycle.

tion was composed primarily of exoskeleton, and so the values would probably approximate those of the carapace. It is apparent that the organic contents of the mid-gut gland, gill, and muscle increased during the proecdysial stages. The greatest inorganic fluctuation was found in the carapace. Only minor alterations were found in the other tissues.

The calcium and phosphorus composition of the carapace, mid-gut gland, gills, muscle, and blood were determined. The results, based on dry weight, are plotted in Figures 4–8. In Figures 4–7, the data are plotted as changes in per cent dry weight. The values for the blood (Fig. 8) are presented as mM/liter.

The organic and inorganic composition of the exuviae were also determined. The results are illustrated in Figure 9. Also contained in this figure are the calcium and phosphorus contents of the exuviae, expressed as per cent composition.

The organic, inorganic, and calcium contents of the entire exuvia were compared with those found in the exuvial carapace; this information is summarized in Table 1. The carapace contained less organic material and less calcium than the entire exuvia. The mount of inorganic

FIG. 3. Changes (mean ± S.E.) in the inorganic content of four tissues of *P. vigil* during the molt cycle.
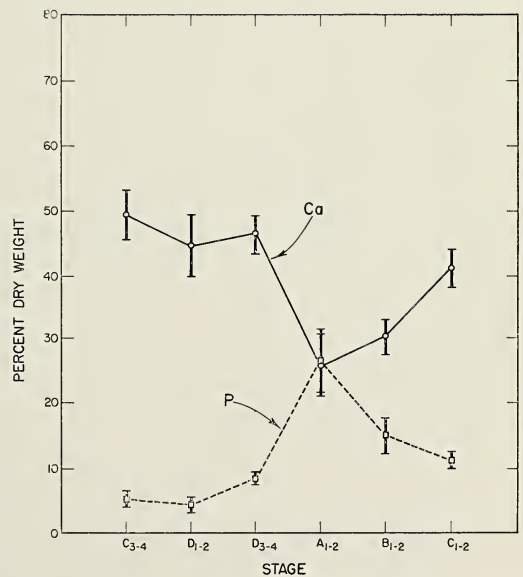
FIG. 4. Calcium and phosphorus content (mean ± S.E.) of the carapace of *P. vigil* during the molt cycle.
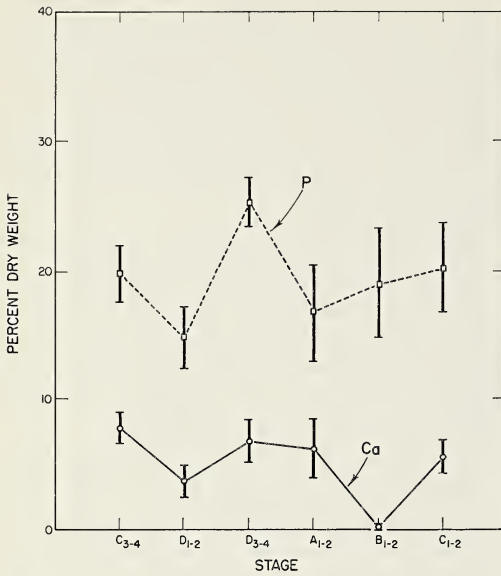
FIG. 5. Calcium and phosphorus content (mean ± S.E.) of the gills of *P. vigil* during the molt cycle.
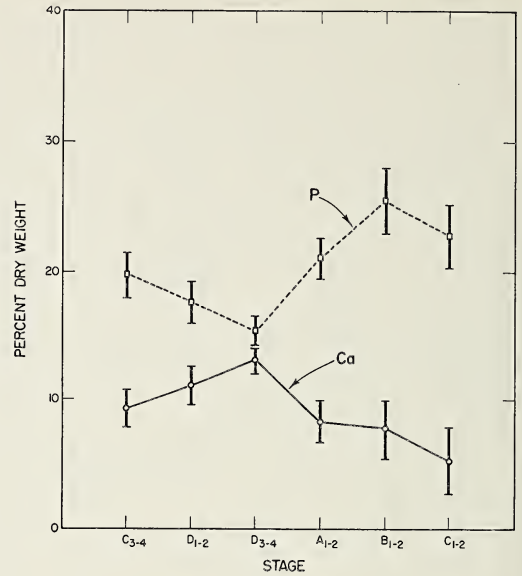
FIG. 7. Calcium and phosphorus content (mean ± S.E.) of the mid-gut gland of *P. vigil* during the molt cycle.
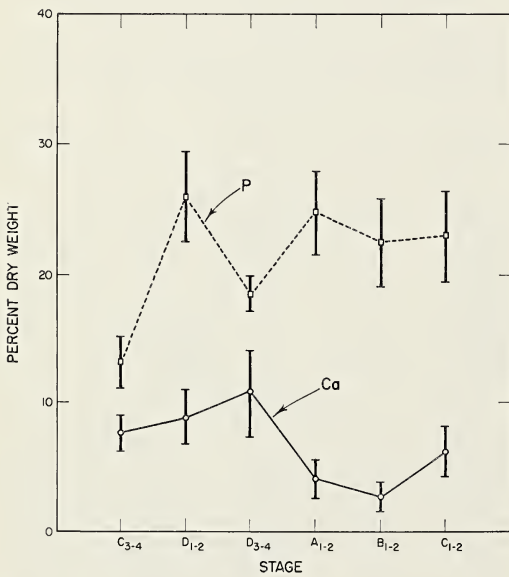
FIG. 6. Calcium and phosphorus content (mean ± S.E.) of the muscles of *P. vigil* during the molt cycle.
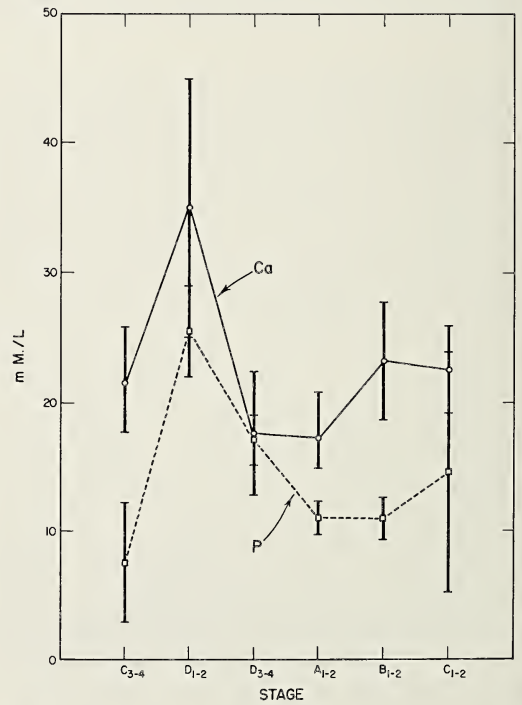
FIG. 8. Calcium and phosphorus content (mean ± S.E.) of the blood of *P. vigil* during the molt cycle.
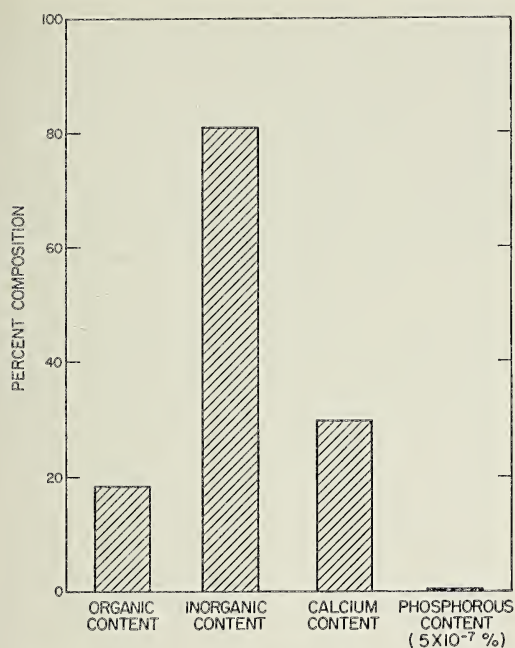
FIG. 9. Percent composition of the exuvia of *P. vigil* (values based on dry weight).

matter in the carapace was greater than that in the entire exuvia.

To determine whether larger crabs were able to resorb the same amount of calcium as smaller crabs, the amount of calcium in the exuviae was plotted against exuvial carapace width. (The data were then statistically analyzed for regression and the slope was fitted by the least squares method.) Figure 10 clearly indicates that as the crabs increased in size the amount of resorbed calcium decreased, and the regression analysis showed that the calculated slope was 0.082 ($P < 0.001$).

DISCUSSION AND CONCLUSIONS

Weight Changes During the Molt Cycle

Changes in weight of Crustacea during ecdysis are due to absorption of water (Baumberger and Olmsted, 1928; Drach, 1939; Needham, 1946; Guyselman, 1953; Travis, 1954). The alterations of body weight and water content of *P. vigil* have been reported elsewhere (Sather,
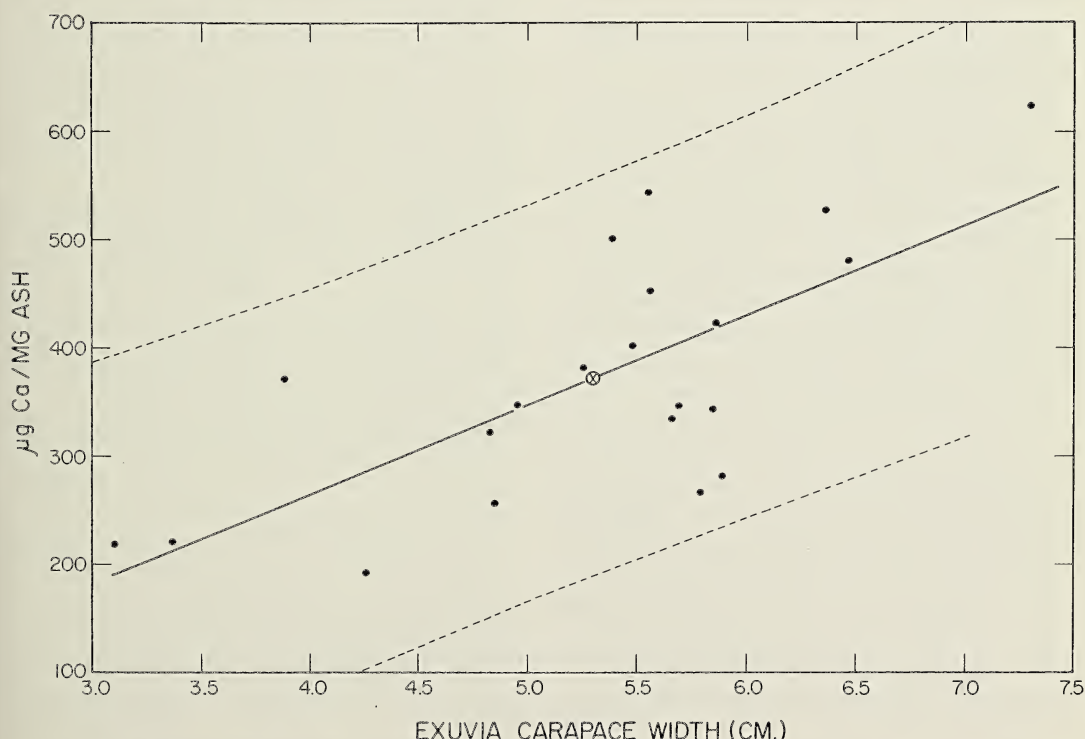
FIG. 10. Regression of calcium content of exuviae on exuvial carapace widths of *P. vigil*. b = 0.082 ($P < 0.001$). Upper and lower curves represent the 95% confidence limits.

1966). In brief, during proecdysis the crabs have a tendency to lose weight, which can be attributed to a loss of water. Between D_3 and D_4 the mean weight gain was about 8%. The weight change between D_4 and A_1 was an insignificant loss of 1.5%. However, the crabs gained 18.8% between A_1 and A_2. No significant weight alterations were noted between A_2 and B_1, B_1 and B_2, and B_2 and C_1. Between stages C_1 and C_2 the weight gain was 4.4%. No significant changes were found during the remainder of the molt cycle. However, the overall weight gain between two successive intermolt stages was approximately 34%.

The total water content of the crabs during the ecdysis cycle was also followed. During the premolt stages, the crabs tend to become dehydrated; the water lost at D_{1-2} and D_{3-4} was calculated to be 8.1% and 7.7% below the C_4 water content of 70%. The postmolt water content was increased from about 62% (D_{3-4}) to 77% (A_{1-2}) and 75% (B_{1-2}), but these water content changes were statistically not significantly different from the intermolt value of 70.3%.

Water Content of Four Organs and "Remainder" Throughout the Molt Cycle

The amount of water in the various tissues of a crustacean during the molt cycle has not been previously reported. The water content of the carapace, mid-gut gland, gills, muscles, and "remainder" in *P. vigil* is illustrated in Figure 1. (The values are the means ± S.E.) Analysis of variance on the arcsin transformed values illustrated that interaction was present, showing that the water content of the tissues did not vary uniformly throughout the molt stages.

The greatest fluctuations in water content were found in the carapace during ecdysis. A decrease of about 5% was noted during the proecdysial stages, but this was not statistically significant. The gain in water content between D_{3-4} and A_{1-2} was a significant gain of about 37%. Although the extracellular fluid volumes were not determined, this gain could possibly reflect a greater extracellular fluid volume. During the B_{1-2} and C_{1-2} stages, the water content was decreased to 20.54%, which was caused by the incorporation of calcium salts.

The alterations in gill hydration are repre-

sented as the top curve in Figure 1. During the premolt stages, the gills lost 4.57% of their water content—a significant decrease. After ecdysis the gill water content was increased to about 87.64%, which was found to be a significant gain. The hydration at B_{1-2} was increased to a significant 89.42%. The per cent hydration of the gills during the C_{1-2} period was not significantly different from that at the C_{3-4} duration (90.20%).

Robertson (1960) has demonstrated that the gills of *Carcinus maenas* were the site of water and ion absorption but that the antennal glands were the sites for the loss of the water and the ions. Because the urine of *P. vigil* was not sampled, it is not possible to exclude these glands and the gills as the sites of water flux.

The decrease in water content of the muscles during the premolt stages from a value of 85% to 76% was found to be significant, as was the increase to 82% at the A_{1-2} periods. The further increases during postecdysis were not significant.

The same type of pattern is seen to occur in the mid-gut gland. The intermolt water content was found to be 85.16%. The reduced hydration during the premolt stages to about 68% was a significant drop. During the A_{1-2} duration, the water content was increased to 78.24%. The subsequent changes observed during postmolt did not differ significantly.

Excluding the carapace and the remainder, the increase of about 11% in the mid-gut gland during ecdysis was the greatest alteration. Robertson (1960) reported that in *C. maenas* the water content of the mid-gut gland and its fluid increased during the early postmolt stages. This was attributed to absorption of water via the fore-gut. The results reported here for *P. vigil* are consistent with those reported by Robertson (1960) and also with the findings of Drach (1939) for *Maia squinado* and *Cancer pagurus*.

The fluctuations of the "remainder" during the molt cycle are also illustrated in Figure 1. It is quite obvious that this portion also lost some water during proecdysis. The intermolt water content was calculated to be 68.69%, and postecdysial values of about 65% were significantly different from the former. After ecdysis the water content rose to a significant high of 83.18%. No statistical difference was found

between the A_{1-2} and B_{1-2} values. During the last two postecdysial stages, the water content decreased to 77.78%. Because the "remainder" was largely composed of exoskeleton, this curve follows the same general pattern as the carapace. The increase in hydration following ecdysis was probably due to a greater extracellular fluid volume of the exoskeletal tissues. During calcification, the extracellular water was undoubtedly replaced by calcium salts.

The water content of the whole blood during the premolt stages of *P. vigil* was not determined. Water is not absorbed during the first three proecdysial stages (Sather, 1966). Travis (1954, 1955b) demonstrated that the premolt water uptake by *Panulirus argus* was limited to 15 minutes just prior to ecdysis. However, as can be seen in Figure 1, *P. vigil* becomes desiccated during proecdysis. The water content of the intermolt blood was found to be 94.14%. The value for the A_{1-2} stages was 93.98%; at B_{1-2}, 91.46%; and at the C_{1-2} period, 93.88%. Because the greatest absorption of water occurs during the period immediately following ecdysis, it would be expected that the blood at the A_{1-2} duration would be somewhat diluted (to be explained below). Travis (1955b) found that the blood calcium and phosphorus concentrations of *P. argus* were decreased following molt. Robertson (1960) reported that in *C. maenas* the concentrations of blood constituents were reduced during the early postmolt stages. Both authors attributed their findings to the uptake and retention of water.

Proecdysial and early postecdysial *P. vigil* exhibit significant alterations in water content. This phenomenon offers a fine thesis problem on the osmoregulatory mechanisms and modes employed by the crab during this "stressed" duration.

Organic Content of Four Organs Throughout the Molt Cycle

The organic content of the carapace, gills, muscle, and mid-gut gland are plotted in Figure 2. Analysis of variance illustrated that the organic content of the organs did not uniformly fluctuate.

A great variability is seen in the organic content of the carapace, but none of the alterations

was found to be significant from the intermolt content of 35.76%.

The organic composition of the mid-gut gland increased from an intermolt value of about 10% to approximately 25% at the premolt stages. This accounts for the hyperglycemia reported for proecdysial *Panulirus japonicus* by Scheer and Scheer (1951). After ecdysis, the organic value dropped to 16.15%, which can be similarly attributed to the loss of reserves utilized for the active process of molting and for the tanning of the pigmented layer, especially as the crabs do not feed until the late B stage. The value found at the C_{1-2} period was not significantly different from that of the previous period, but it was greater than that of the C_{3-4} stages. During the early C stages, *P. vigil* becomes voracious, obviously to compensate for the loss which occurred during ecdysis.

The alterations in the organic content of the muscle were similar to those of the mid-gut gland. From an intermolt level of 11.66%, the organic content increased to about 20% during proecdysis. The significant increase in organic material during these periods probably is due largely to the accumulation of glycogen to serve as an energy source for the epidermal cells which form the proecdysial tissues and the molting fluid. It is quite possible that the muscle organic constituents would be at a high level just prior to ecdysis, as the active process of exuviation would require a great amount of energy. In addition, crabs in the early D_3 stage did feed and the resulting energy would have to be stored either in the mid-gut gland or in some other tissue. Undoubtedly, the former has a saturation level and the most likely tissue, therefore, would be the muscle because of its adequate blood supply.

The lowest curve in Figure 2 illustrates the changes in the organic content of the gills. The minimum concentration of organic materials occurred in the intermolt period (6.51%) and the highest (10.45%) was found to occur in the D_{3-4} stages. The premolt gains were significantly greater than the intermolt value. During the postecdysial stages, the gill organic content decreased to the original intermolt content.

One possible explanation for the observed increase in gill organic content at D_{3-4} would be

that a supply of energy would be required to regulate the ionic ratio of the internal to external media. Unfortunately, the glycogen content of the gills was not determined. Considering the decreased water content of *P. vigil* during late premolt, it appears that the gills may be possible sites of water and/or ion efflux. This hypothesis is not in agreement with the report by Robertson (1960), which stated that the antennal glands of *C. maenas* were the sites of water and ionic efflux. One possible method for determining the site of water flux in *P. vigil* would be the use of tritiated water. Radioisotopes representing the extracellular ions would also verify the sites of ionic flux.

Because the organic content of premolt blood was not determined, it was not possible to follow the changes throughout the ecdysis cycle. The organic constituent during the A_{1-2} period was 2.93% of the whole blood. The content in stages B_{1-2} was 4.02%; in the C_{1-2} stages, 2.86%; and in the C_{3-4} stages, 2.64%. The observed increase during the B period may be due to the commencement of food ingestion and the subsequent loss (during the C stages) by the distribution to the mid-gut gland and exoskeleton.

Inorganic Content of Four Organs Throughout the Molt Cycle

The fluctuations in inorganic content are illustrated in Figure 3. Analysis of variance indicated that interaction was again present.

As could be expected, the carapace varied much more in inorganic content than did the other sampled tissues. The intermolt value was determined to be 42.12%. The significant increase to 52.01% during the D_{1-2} stages possibly can be attributed to the formation and tanning of the new epicuticle. However, the inorganic constituent in the proecdysial tissues is not dominantly calcium (see Fig. 4). The finding is in agreement with those of other investigators (Drach, 1936, 1939; Krishnan, 1950; Travis, 1955a, 1960, 1963). During the D_{3-4} stages when resorption was nearly completed, the inorganic content was decreased significantly to 43.80%. It becomes apparent that the entire carapace is not an area where maximum resorption occurs (see introductory remarks). Following ecdysis the inorganic content

of the carapace was approximately 20%, reflecting the amount found in the exocuticle. During the A_{1-2} periods, the exocuticle was impregnated with calcium salts, with concomitant formation of the principal layer. During the B_{1-2} and C_{1-2} stages, periods of major calcification, the inorganic composition was increased to 27.31% and 41.28%; both were significant gains. The amount during the early C periods approximated that of the intermolt content.

The mid-gut gland's alterations are plotted also in Figure 3. The increased values during premolt (D_{1-2} = 5.98%, D_{3-4} = 7.74%) were statistically different from each other and also from the intermolt value of 4.29%. This was probably due to the storage of some constituents absorbed from the exoskeleton. Similar storage has been reported by Paul and Sharpe (1916) for *Cancer pagurus;* by von Schönborn (1912) and Robertson (1937, 1960) for *Carcinus maenas;* by Drach (1939) for *Maia squinado;* by Kincaid and Scheer (1952) for *Hemigrapsus nudus;* and by Travis (1955a) for *Panulirus argus.* The reduction in inorganic content during the postmolt stages can be attributed to the redistribution of the stored elements to the hardening exoskeleton.

The gill inorganic content was found to vary slightly. The observed value of 4.15% at the D_{1-2} duration was found to differ significantly from those of the other durations. The greater inorganic content was due to the formation of the proecdysial tissues, which similarly occurred in the carapace, i.e., the epicuticle and exocuticle.

As expected, the mean per cent inorganic composition of muscle did not vary significantly between stages ($P > 0.05$). The average content of the inorganic materials was 2.44%, the range being 2.14–2.69%.

The intermolt inorganic composition of the whole blood was 3.22%. During the A_{1-2} period it was 3.09%, and at the B_{1-2} it was 4.52%. The former value reflected the absorption of sea water, and the latter value was probably due to the mobilization of calcium, after it was actively transported by the gills to the exoskeleton. The blood inorganic content at the C_{1-2} period was approximately equal to the intermolt value, indicating that the sclerotinization process was nearly completed.

Calcium and Phosphorus Contents of Five Organs Throughout the Molt Cycle

The calcium and phosphorus contents of the carapace, gills, mid-gut gland, muscle, and blood were determined. The values, based on per cent dry weight, are plotted in Figures 4–8. The blood data are given in mM/liter. Interaction analyses on the organs' calcium and phosphorus contents were positive (P < 0.01).

The intermolt carapace calcium content (Fig. 4) was 49.51% and the phosphorus content was only 5.42%. Both of these values are large in comparison with those reported by Prenant (1928) for five species of crabs in temperate waters. His data (per cent calcium and phosphorus, respectively) were: *Carcinus maenas*, 30 and 2; *Maia squinado*, 31 and 2; *Portunus puber*, 36 and 2; *Cancer pagurus*, 36 and 0.8; *and Xantho floridus*, 38 and 0.4. However, as noted by Vinogradov (1953), the majority of these values were only relative. Hayes, Singer, and Armstrong (1962) reported that the carapace calcium of the lobster, *Homarus vulgaris*, was 25.2% and the calcium content of the claw was 23.8%. The phosphate contents of these two anatomical areas were reported to be 1.33% and 2.05%. The lower calcium content of temperate species may be a genetic difference or may be caused by a lesser availability of this environmental element. Unfortunately, this latter possibility cannot be checked because calcium data at the collection sites were not available. The environmental calcium content certainly influences the amount absorbed by an organism, as well as the amount retained. It is known that the total calcium content of fresh water crustaceans is less than that in marine species.

The calcium alterations of the carapace during the molt cycle are illustrated in Figure 4. Preceding molt, the calcium content varied only slightly during the D periods. After ecdysis (A_{1-2}) the calcium content was diminished to 26.04% and reflected the amounts in the epicuticle and pigmented layers. Between B_{1-2} and C_{1-2}, which was the major duration of calcification, the calcium content was increased significantly to 41.12%, which was similar to that of intermolt.

The phosphorus changes of the carapace are also illustrated in Figure 4. The content at C_{3-4} was calculated to be 5.42%, which is much greater than that found in *Panulirus argus* by Travis (1957). In *P. argus*, in late stage C, about 3% of the total integument was composed of $Ca_3(PO_4)_2$, which is approximately 0.2% of the total phosphorus. In *P. vigil*, a small insignificant increase was observed during the last proecdysis stages. At stages A_{1-2}, the phosphorus content was increased to 26.76% of the dry weight, which was about the same as the calcium concentration. This localization could have been due to the mobilization of phosphorus by the blood. Travis (1957) has demonstrated that the postecdysial integument stains heavily for alkaline phosphatase. Thus, a much greater amount of phosphorus would be present than during the other stages. It is thought that alkaline phosphatase liberates phosphates which combine with calcium to form the calcium phosphate complex. The high phosphate content during the A stages causes one to ponder over its significance, because the major anionic constituent of the intermolt integument is carbonate and not phosphate. In *P. vigil* during the first C periods, the phosphorus content decreased significantly to 11.34%. This reduction can be attributed to the increased deposition of calcium salts.

The fluctuations in gill calcium are plotted in Figure 5. No significant differences were found between the intermolt value of 7.88% and the first premolt values. However, the decreased value of 0.30% at B_{1-2} did differ significantly from the other values. Because the B_{1-2} period is the initial duration of greatest calcification, a high gill permeability, caused by calcium, would be greatly detrimental for extraction of calcium from the medium. Robertson (1960) demonstrated that a great influx of calcium occurred during postmolt in *Carcinus maenas*. Unfortunately, the amount of calcium in the gills was not measured. It appears, then, that in *P. vigil* the mechanism to increase the movement of calcium into the animal serves to reduce the gill calcium content, allowing calcium to enter across the gills at a more rapid diffusion rate, the blood then mobilizing the element to the integument.

The phosphorus content of the gills during the molt cycle is illustrated in Figure 5. The

intermolt value was calculated to be 19.80% of the dry weight. Analysis of variance illustrated that there were no significant differences among the means. However, there is a suggestion that the gills may store phosphorus during the D_{1-2} stages. This suggestion is reinforced by the gill organic content at D_{1-2} (Figure 2). The phosphorus content may be indicative of an energy-requiring process for early postecdysial absorption of sea water.

Figure 6 demonstrates the alterations of calcium and phosphorus content of the muscle throughout the molt cycle. The calcium concentration increased from 7.70% at the C_{3-4} period to 10.72% at the D_{3-4} stage. Following ecdysis the calcium content was reduced to 4.14%, and at the B_{1-2} period it was further reduced to a significant 2.72%. During the period when the majority of calcification occurred (between B_{1-2} and C_{1-2}), the muscle calcium was raised to 6.28%.

During the process of exuviation, i.e., the time when active musclar contractions occur to facilitate withdrawal of the crab from the old exoskeleton, a large amount of energy would be required. As can be seen in Figure 2, the organic content of this organ also increased. Another requirement would be an ample supply of calcium to expedite muscular contractions. Calcium and organic reserves may be localized in this organ to insure proper exuviation. This phenomenon would then favor the survival of the crab during the process of ecdysis. The muscles, in addition to the mid-gut gland, may also serve as a place for calcium storage.

The 6.58% decrease in calcium between the D_{3-4} and A_{1-2} periods may be due to the mobilization of the element to the exocuticle; during the first postecdysial stages, the latter is impregnated with and concomitantly hardened by calcium salts (Travis, 1960, 1963).

The muscle phosphorus content was greater than that of calcium; phosphorus is the most important element in muscle contraction. The values at D_{1-2} (25.98%) and A_{1-2} (24.82%) were significantly different from the intermolt content of 13.14%, but the former values were not statistically different from each other. The loss of phosphorus during D_{3-4} may have been due, in part, to the mobilization to the gills and carapace, but 2.67% cannot be accounted for.

The reasons discussed in the above paragraph seem to be applicable to phosphorus as well as to calcium. However, the suggestion that proecdysial storage of phosphorus in the muscles occurred is indeed very weak.

On examination of Figure 6, it can be seen that phosphorus and calcium are controlled differently. After ecdysis the amount of calcium in the muscles is diminished, but the phosphorus content remains relatively constant.

The phosphorus and calcium fluctuations in the digestive gland are seen in Figure 7. As found in the alterations in carapace calcium and phosphorus (Fig. 4), the curves tend to be reciprocal to each other. But the mid-gut gland phosphorus content was always greater than that of calcium. Significant differences among the means did exist ($P < 0.01$).

The intermolt calcium content of 9.31% did not differ significantly from that at D_{3-4} (13.05%). However, the gain suggests that some calcium is stored in the mid-gut gland during premolt. After ecdysis some of the calcium (5% in *P. vigil*) may be used for calcification of the exocuticle. These observations are consistent with the reports of Paul and Sharpe (1916), von Schönborn (1912), Drach (1939), Kincaid and Scheer (1952), and Travis (1955a), but are inconsistent with that of Robertson (1960), who reported that in *C. maenas* the mid-gut gland secretion during postmolt (stages A and B) had about 16% more calcium than it did during intermolt.

The phosphorus content decreased from 19.76% in C_{3-4} to 15.28% in the late D stages and increased to 21.04% and 25.50% during the A_{1-2} and B_{1-2} stages, respectively. The postecdysial gain may have been due to mobilization from the gills (Fig. 5), which lost approximately 10% during postmolt. It is obvious that this gland in *P. vigil* does not store phosphorus during the premolt periods, but it does appear that the gland becomes a phosphorus reservoir after ecdysis. This finding is inconsistent with the reports by Travis (1955b, 1957) that phosphorus was stored in the midgut gland of *P. argus* prior to ecdysis, but that following molt, the phosphorus content rapidly decreased. The latter conclusion was based primarily on histochemical observations and

blood analysis, and no chemical analysis of the mid-gut gland was undertaken.

A question arises after examining all of the phosphorus curves. Because the crabs were not feeding during the A and early B stages, where did the phosphorus originate? From Figure 5 it is seen that the phosphorus content of the gills is drastically increased during the D_{3-4} stages. Following ecdysis the phosphorus content of the organ was reduced by approximately 9%. The phosphorus content of the mid-gut gland from D_{3-4} to A_{1-2} was increased by about 6%. Therefore, possibly the gills, rather than the mid-gut gland, serve as a phosphorus reservoir. Another possible source for the accumulation of phosphorus could be the water that was imbibed immediately following ecdysis. However, this is not likely because a pilot experiment demonstrated that phosphorus is not accumulated during and following ecdysis. The application of the radioisotope P^{32} could be very useful in resolving this question.

Figure 8 illustrates the calcium and phosphorus contents of the blood during the molt cycle. The data are plotted on a volume basis, as is shown on the ordinate. The blood calcium and phosphorus levels tend to be parallel throughout the molt cycle.

During the D_{1-2} periods, the blood calcium was significantly increased to 35.09 mM/liter from the C_{3-4} content of 21.58. A significant decrease to 17.68 mM/liter was observed at the D_{3-4} stages. In *Panulirus argus*, Travis (1955b) also noted a premolt blood calcium increase, followed by a decrease in the late premolt stages. The loss was attributed to dilution when the lobster took in water. During the A period, the lobster's blood calcium was at the intermolt value. The content was slightly increased at the B stages and, following this interval, i.e., during the C period, the concentration was decreased below the intermolt value. In late premolt *Carcinus maenas*, Robertson (1960) also noted a blood calcium increase of about 21%. Within 24 hours after molting (Stage A), the blood calcium content was reduced by approximately 25%. In 2 to 14 days following ecdysis, the blood calcium was further reduced to approximately 31% of the intermolt value.

The water content of *P. vigil* decreases during proecdysis (Sather, 1966). Also, as evidenced from inspection of the changes in water content of sampled organs (Fig. 1), dehydration definitely occurred during the premolt stages. The first decrease in water content was found during the D_{1-2} period. This would account for the rise in the blood calcium at this interval. The observed reduction at the D_{3-4} stages is not due to the uptake of water. On a volume basis, the amount lost was calculated at 17.41%. However, on a dry weight basis, this loss was only 2.04%. The blood must have lost some calcium to other organs or the external medium. Thus, the calcium may have been distributed to the muscles and/or the mid-gut gland. The large standard errors ($\pm$ 1.2%) for the latter two organs do not permit an accurate estimate of the quantity accumulated by each organ.

Following ecdysis, no significant changes in the blood calcium were observed. As seen in Figure 1, the greatest increase in water content occurred at this time. It should be recalled that the water taken in was sea water, including the elements present in the medium. This has been verified by the studies of Robertson (1960). Thus, a great calcium dilution would not be expected. Also, as seen in Figures 6 and 7, the mid-gut gland and muscle lost some calcium which could have been accumulated by the blood. At period B_{1-2} the blood calcium was increased to 23.23 mM/liter. This could have been due to absorption of calcium, via the gills, from the environment. Figure 5 illustrates that at this interval the gill calcium was drastically reduced, increasing the efficiency of extracting calcium from the external medium.

Thus, except for the effect of dehydration at the early proecdysial stages, the calcium content of *P. vigil* blood remains more stable than in other investigated crustaceans. This fact may be due to the nearly chemically constant environment of the crab. Except for one month, the environmental salinity and calcium was not less than 34 0/00 and 300 mg/liter, respectively (Sather, 1966).

The total phosphorus fluctuations of the blood during the molt cycle are also depicted in Figure 8. The significant increase of blood phosphorus to the D_{1-2} interval of 25.52 mM/liter can be attributed to the desiccation of the animal. The reduction found at D_{3-4} (17.19

mM/liter) possibly reflects the relocation of phosphorus to the gills (Fig. 5). At stage A_{1-2}, the value was slightly greater than the intermolt value. This decrease can be assigned to dilution, i.e., by the uptake of water from the environment. In sea water, phosphorus is present in much smaller quantities than is calcium. The annual average phosphate content of sea water was less than 1 µg/liter (Sather, 1966). Also, the results of a preliminary experiment illustrated that the phosphorus content of the external medium was increased when containing molting and postmolt crabs. The leveling-off of the blood phosphate at B_{1-2} and the increase at C_{1-2} was probably due to the resumption of feeding. The majority of *P. vigil* began to feed at B_2 and only occasionally when they were in the B_1 stage.

Homarus americanus (Hollett, 1943), *Panulirus argus* (Travis, 1955*b*), and *Carcinus maenas* (Robertson, 1960) also increased their blood phosphorus during the premolt stages. Travis (1955*b*) found that after ecdysis, the phosphorus content steadily decreased. This was attributed to a depletion of phosphorus by calcification of the exoskeleton concomitant with a reduction in the stored mid-gut gland phosphorus. Robertson (1960) reported that within 24 hours after ecdysis the blood phosphorus of *C. maenas* was slightly less than the intermolt value. Within 2 to 14 days after molting the value was increased to about 22% above that of the intermolt level. The report of Drilhon (1935) is not consistent with the above reports, in that the phosphorus content of the blood of premolt and postmolt *Maia squinado* was not altered.

Composition of the Exuviae

The discarded exoskeleton or exuvia of *P. vigil* is not consumed by the crab as it is in the insects. Robertson (1937) reported that the exuvia of *Carcinus* comprised about 46.2% of the total dry weight. Lafon (1948) stated that the value was 47.5% of the dry weight. These calculations were not made on the exuviae of *P. vigil*, but the percentages of organic, inorganic, calcium, and phosphorus contents were determined and these data are given in Figure 9. The per cent composition was based on the dry weight. The histogram illustrates

that about 81% of the entire exuvia was composed of inorganic material and only approximately 37% of the inorganic content was due to calcium. Odum (1957) reported that the calcium content of the exuviated chela of *Uca pugnax* was 27.7% of the dry weight, which is somewhat consistent with the calcium content of the exuvia of *P. vigil*.

Knowing the amount of calcium in the exuvia (30%) and assuming that the intermolt carapace, which contained about 50% calcium, is representative of the entire exoskeleton, it is possible to calculate the quantity of calcium resorbed, which is about 20%. The amount of calcium stored in the mid-gut gland and the muscle was approximately 7%. Thus, the quantity stored and resorbed closely approximates the amount of calcium (26%) present in the early postmolt carapace. The increase in amount (23%) between A_{1-2} and C_{3-4} undoubtedly is acquired from the environment.

The phosphorus content of the exuvia was found to be only approximately $5 \times 10^{-7}\%$ of the dry weight. Unfortunately, comparable phosphorus data for other species have not been reported. Employing the above mathematical deductions, it would seem possible to account for the phosphorus budget. However, such a process produces a deficit of about seven magnitudes. It is possible that the reproductive system and the gastrointestinal tract, which were not sampled, may have been highly selective for the storage of this element. The great resorption of phosphorus is obvious and it must have been stored, because the results of an experiment showed that proecdysial and postecdysial crabs lose very little phosphate (2.6–5.1 µg PO_4) to the environment.

The organic content of the exuvia was found to be only 18.7%. This organic material has been reported to be composed of lipo-protein, chitin, mucopolysaccharides, and proteins (Travis, 1955*a*, 1957, 1963; Dennell, 1960). The amount of organic material resorbed was about 17%, which is consistent with the amounts stored in the mid-gut gland and muscle.

Neto (1943) reported that the calcium content of the carapace of *Uca maracoani* decreased as its breadth increased. The calcium content of the exuviae of *P. vigil* was compared with the width of the cast exoskeletons. Figure 10

clearly demonstrates that less calcium is re-sorbed from the exoskeleton as the crab in-creases in size. The calculated slope was found to be 0.082, which indicates an increase of approximately 82 µg Ca/mg ash for each centimeter increase in breadth. The slope dif-fered significantly from 0 (P < 0.001). A similar analysis was performed, comparing the amount of carapace calcium with the wet weight of the C_4 crabs. The results, which are not illustrated in this report, demonstrated that regression did not occur and that the calculated slope was 0.0009. Thus it appears that less cal-cium is resorbed by large crabs and, therefore, more calcium appears in the exuvia. This phe-nomenon illustrates the effects of ageing on one physiological process of an invertebrate. It may be possible that the enzymatic activities responsible for crustacean decalcification are decreased with age and those required for recalcification are not influenced by senescence. A study of the alkaline phosphatase and car-bonic anhydrase activities of the epidermal cells may verify the above observations.

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On Some Gastrocotyline (Monogenoidean) Parasites of Indian Clupeoid Fishes, Including Three New Genera

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ABSTRACT: Seven species of monogenetic trematodes, including the two geno-types, *Engraulicola forcepopenis* George, 1961 and *Engrauliscobina thrissocles* (Tripathi, 1959), are recorded. All seven of these atypical gastrocotylines belong to the subfamily Gastrocotylinae s.s. and are parasitic on clupeoid fishes. Four species in the present collection, viz., *Engraulicola micropharyngella* sp. n., *Engraulixenus malabaricus* gen. et sp. n., *Engrauliphila grex* gen. et sp. n., and *Engrauliscobina triaptella* sp. n., were collected from fishes of the family En-graulidae, while an entirely new type, *Pellonicola elongata* gen. et sp. n., was obtained from Clupeidae. The tendency to unilateral inhibition of the clamp rows is incomplete in all these atypical gastrocotylines, and all are characterised primarily by their clamp structure. Diagnostic characters, with special reference to the haptor (its adhesive units or clamps and anchors), the male terminalia, vaginal complex, and other salient features which appear to be taxonomically important, are given for each species.

SOME GASTROCOTYLID WORMS have been found on the gills of clupeoid fishes at Mandapam Camp. Their clamp structure shows them to be allied to *Gastrocotyle* and *Pseudaxine*. The tendency to develop a unilateral haptor is another common feature. But of the 32 known species of Gastrocotylidae, and 8 new species described by me (in press), all 40 are parasitic on scombroid fishes (including Carangidae). Indeed, it is usual to find these more highly evolved Monogenoidea on the more highly evolved fishes, while the simpler clupeoids are typically parasitized by Mazocraeidae. The occasional excursions across the phylogenetic trees of the hosts for each of these families of parasites have been discussed by Sproston (in press). The present collection adds support to her hypothesis, since it contains four new forms from Engraulidae and one entirely new type from Clupeidae. Collection and treatment of specimens was performed as described in a previous paper (Unnithan, 1957:28–29).

All of these atypical clupeoid parasites belong to the subfamily Gastrocotylinae *sensu stricto,* hitherto containing only *Gastrocotyle* v. Ben. et Hesse, 1863, *Chauhanea* Ramalingam, 1953, and *Yamaguticotyla* Price, 1959. They are characterized primarily by their clamp structure (Unnithan, 1967b). There are paired braces in the posterior region of the clamp capsule, as in all Gastrocotyloidea (as distinct from Microcotyloidea), but the clamps themselves are bilaterally symmetrical; and, unlike the subfamily Priceinae, for instance, to which *Pseudaxine* belongs, there are no complex dorsal shields to other sclerites developed in the dorsal wall of the capsule in association with the median spring, nor are there riblike thickenings in the capsule walls. While in *Gastrocotyle* spp. the ventral arm of the spring is often doubly bifid, its ends sometimes form articulated struts to the jaw rami. This condition is not found in the other genera. In all of them (with the doubtful exception of *Chauhanea* and *Yamaguticotyla*), the dorsal arm of the spring bears a forked appendix associated with noncuticularized ligaments, presumably a transitional condition to that in Priceinae.

The tendency to unilateral inhibition of the clamp rows is complete in *Gastrocotyle* spp. (also in *Pseudaxine* in Priceinae and in some

Axinidae), but it is incomplete in all the atypical clupeoid parasites described in the present study.

The partition of genera is based on criteria which have appeared to be valid for genera of other subfamilies of the higher Monogenoidea, namely:

(1) The relative encroachment of the clamp rows up the body proper (as distinct from a tail-like haptor quite distinct from the body, for example in *Chauhanea*), which determines the *zone of pivoting* in all the possible feeding attitudes of the attached worm. If this pivoting zone occurs in the thicker gonad zones, then the torque set up will tend to a somatic asymmetry (e.g., *Engrauliscobina*); if, on the other hand, it is near or beyond the end of the testes zone (as in *Engraulicola, Pellonicola,* and *Pseudaxine*), then the highly contractile body may be irregular in outline at any one moment, but very little permanent strain would be registered, and there is no structural asymmetry in the body proper. Nor is this asymmetry present in forms where the pivoting zone occurs anterior to the gonad zone: the fore-body alone in these forms is free to bend, and again no true somatic asymmetry is developed (e.g., *Gastrocotyle, Engraulixenus,* and *Engrauliphila*).

(2) The degree of suppression of one side of the haptor. It is considered that there is a greater difference between complete suppression and the inhibition of all but one, or of all but two or three clamps, than between inhibition of only about half the clamps.

(3) The form of the anchors, as has been shown by Llewellyn (1957: Figs. 22 and 23 for *Gastrocotyle* and *Pseudaxine,* and similarly in 1959: Figs. 8 and 9), is regarded as a generic character. The useful differences are the relative lengths of the handle (main root) and hook, of the spur (secondary root), and the approximate segment of a circle represented by the sickle-like hook. These characters are fundamental, since they are developed in the postlarval stages of the onomiracidium, and persist throughout life unless anchors are shed. The persistence of other larval anchors may be a specific character.

(4) Additional sclerites associated with the penis, e.g., the peculiar forceps on the penis

head. The only possible analogue is found in *Heterapta* Unnithan, 1961 (Heteromicrocotylidae), where the two spines appear to have a much deeper origin and are straight and much longer, probably functioning as vagino-dilators.

(5) The occurrence of a single median dorsal vagina, or of paired vaginae opening laterally, at various levels, and their separate confluence into the lateral vitelline ducts, or the intervention of a median duct and, in some cases, the direct course of this to the oötype (as is more usual with an unpaired vagina).

(6) The relative size of the oral pouches and the pharynx (expressed as percentage of mean diameters), and the absolute size range of the latter and its shape.

In view of the possibility of a wide array of related forms being discovered on tropical clupeoids in the future, I hesitate to give formal generic and specific definitions for these new forms, but prefer rather to list their diagnostic characters, with particular reference to the six criteria listed above, and other salient characters which appear taxonomically important in each case.

Engraulicola micropharyngella sp. nov.
Figs. 1–6

Four specimens of this new gastrocotyline were collected from the gills of two mature female *Anchoviella commersonii* (Làcepé.) examined at Trivandrum on August 14, 1957. All of the specimens except the one whole mount figured were broken while staining. The description is based mainly on this well prepared specimen (Fig. 1), but comparative measurements on the broken ones are also included.

Body proper essentially bilaterally symmetrical, anterior and posterior ends narrower; "neck" long and slender, about one-sixth of the total worm; haptor triangular with a short terminal lappet (Fig. 1). Total length 1.3–1.9 mm and maximum width 0.42–0.64 mm immediately in front of the ovary.

Mouth subterminal and crescentic; oral pouches thin-walled, spherical, 16–20 μ in diameter, opening into the buccal cavity; pharynx (unusually) smaller than oral pouches, spherical and thin-walled, 14 μ in diameter (ratio of oral pouch to pharynx = 130%); oesophagus
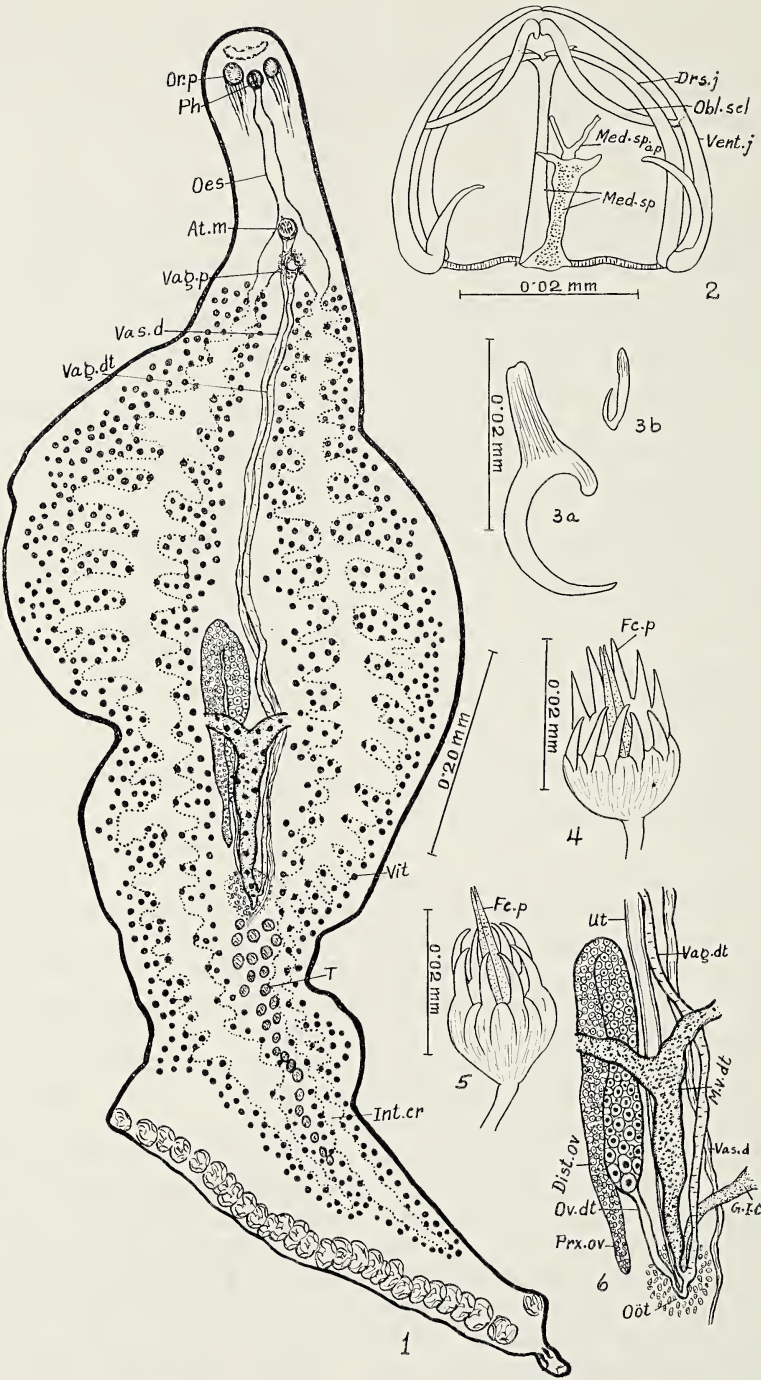
FIGS. 1–6. *Engraulicola micropharyngella* sp. nov. *1*, Complete worm, dorsal view; *2*, clamp, dorsal view; *3a* and *3b*, proximal and distal anchors; *4*, penis with the corona of spines and the forcepiform process; *5*, penis of another specimen; *6*, oötype and ovarian region, dorsal view.

long, narrow, unbranched, and bifurcating into the intestinal crura at the level of the male genital pore; crura with long irregular outer and short simple inner branches; both crura extend into the haptor and terminate at different levels, one extending farther than the other. In the haptoral region the crura are unbranched and the ends are not confluent.

In the specimen examined the haptor bears a long row of 27 clamps on one side, and a single clamp on the other. It is inclined to the body axis at 45°–60°, and is about 35% of the body length. All the clamps are of the same structure, though they vary in size from 16 × 20 μ to 28 × 40 μ. The anteriormost clamp of the long (left) row is the smallest and the single clamp on the right side is more or less of the same size. It is reasonable to expect amphitypy, the long uninhibited row being on the left or right according to the location of the worm on the gill; further collection may show this relationship.

Clamps typically gastrocotyloid in structure: dorsal arm of median spring short and narrow with a thin V-shaped cuticular projection from its distal end; ventral arm of median spring long and narrow, distally bifurcated; base of clamp with a thin, narrow, heavily cuticularized hinge ligament on each side, connecting the median spring with the base or region of articulation of the jaw sclerites; dorsal and ventral jaw sclerites of the two sides symmetrical; dorsal arm of ventral jaw reaches to the level of the bifurcation of the dorsal arm of the median spring; oblique sclerites ("braces") long and narrow, with their distal ends touching in the median line, where their backwardly bent tips form an articulating surface, just within the dorsal jaw (Fig. 2).

Terminal lappet small and cylindrical, 21 μ broad and 36 μ long, demarcated from the rest of the haptor by a small constriction and armed with two pairs of symmetrically placed anchors: anterior pair typically sickle-shaped, 24 μ long, the hook being about three-eighths of a circle. The spur root is short and bent posteriorly toward the point of the sickle, while the handle is less than half the total length (75% of the sickle) (Fig. 3a). It is interesting to note that the spur pointing posteriorly toward the point is also characteristic of the large anchor

of *Gastrocotyle* (Llewellyn, 1957: Figs. 12 and 22). The posterior pair is exceptionally small, with sharply reflexed hooked ends; their overall length is 8 μ (Fig. 3b).

The testes are all postovarian; there are about 27 small spheroidal follicles in 2–3 irregular files extending more or less to the hind end of the shorter intestinal crus or halfway down the haptor. The vas deferens runs forward, curving to the right around the ovarian zone beyond which it becomes median and opens into the base of the penis, apparently without a vesicular dilatation. The atrium masculinus is in the zone of the intestinal bifurcation. The cuplike penis has a thick muscular wall, its rim armed with a corona of 8–10 hooked spines with their tips converging. From the centre of the penis cup on the penis head is a forceps-like, lightly cuticularized structure 13–16 μ long, much longer than the penis hooks, and projecting slightly beyond the penis corona (Figs. 4 and 5). No collar was seen like that described by George (1961) for the genotype.

The ovary is an inverted ∪, its field 210 × 63 μ, situated in front of the testes; its outer longer limb is narrow and the distal inner limb is thicker and contains larger ova. The oviduct arises from the distal end of the ovary, runs backward, and opens into the oötype through a short narrow basal loop (Fig. 6); the uterus arises from the oötype close to the oviduct, runs forward along the median line, and opens near the male genital opening. Eggs spindle-shaped, 40 × 24 μ.

Vitellaria massive, extending from the level of intestinal bifurcation to the tips of each intestinal crus and covering the crural branches, not confluent across the median line; vitelline follicles spherical, 8–10 μ in diameter. The transverse vitelline duct lies at the level of the first third of the ovarian zone, and the median vitelline duct tapers slowly until it reaches the oötype.

The oötype is surrounded by few scattered Mehlis gland cells. The genito-intestinal canal curves toward the right side and opens into the right crus in the midoviduct zone.

The median dorsal vagina is unarmed and is situated in the angle of the intestinal bifurcation, *immediately behind* the muscular unarmed rim of the atrium masculinus and sur-

rounded by small spherical gland cells. The vaginal duct is narrow and runs backward dorsally along the median line parallel to the vas deferens and opens into the vitelline ampulla, independently of the vitelline duct (Fig. 6).

RELATIONSHIPS OF *Engraulicola micropharyngella* SP. NOV.:[2]

1. *Engraulicola* is characterized by the general shape of the body, which resembles a "treed" riding boot, the handle of the boot tree being represented by the slender neck, the main clamp row the sole of the boot (with the metahaptor as the heel), and with the single clamp of the inhibited row suggesting the toe cap of the boot. In other genera a toelike projection is not developed.

 i. In *E. forcepopenis* George, 1961 the foot and toe are nearly at right angles to the body proper and the testes scarcely enter the foot, the zone of pivoting being behind the testis zone. In *E. micropharyngella* sp. nov. the foot is more tapered to the toe and is only 45°–60° to the body axis, and anteriorly a few single-file testes enter the foot and are included in the zone of pivoting. The heel is a little thicker, but no haptoral wing with special gut branches is developed.

 ii. The haptor is less than 50% of the axial length in the genotype, but only about 35% in the new species.

2. In the three larger individuals of *E. forcepopenis* bearing shelled eggs, the haptoral fringe had 44, 39, and 33 clamps, and the two smaller individuals (total length 1.3–1.5 mm) had only 21 and 25 clamps. In the unbroken specimen of *E. micropharyngella* (1.3 mm long), there were 27 clamps; the broken individuals (1.4–1.8 mm long) had 28, 29, and 32 clamps. In all individuals of both species there is a single clamp on the toe cap.

 i. The clamp is wider than long in the former species (length/width = 55–60%), and in the latter is relatively not quite so wide (70%). In both, the soli-

tary clamp is nearly as long as wide, but smaller than those of the other side. The mean diagonal of the solitary clamp in the genotype is 33.2 μ (calculated from the *mean* of the square root of the product of diameters, $\sqrt{1 \times w}$), and that of the new species is only 18 μ, i.e., about 54% of the size of the single clamp in the genotype.

 ii. The appendix of the dorsal arm of the median spring in *E. forcepopenis* is shown as Y-shaped with a short stem. In the present one it is V-shaped with a minute base only, and the posterior ends of the braces are bent back as opposable knobs.

3. Of the two pairs of persistent anchors, the anterior is typically sickle-shaped in both; in *E. forcepopenis* the sickle is about half a circle and the hook nearly equal, but in *E. micropharyngella* the sickle is only about three-eighths of a circle and the length of the handle is only about 75% that of the sickle. The total length of the anterior anchors in the former is 29 μ, and 24 μ in the latter. The posterior simple, hooked anchors are much smaller in the new species (13.6 μ and 8 μ, respectively).

4. The forceps on the penis head are practically identical in both form and size, but the collar observed in the genotype, projecting ventrally from the atrium masculinus, has not been seen in the present material, where the rim of the atrium is a simple flat muscular ring.

 i. In *E. forcepopenis,* though it is larger, there are barely half the number of testicular follicles that are present in the new species. *E. micropharyngella* has no parovarian follicles, while one or two are found in *E. forcepopenis.*

 ii. The spines of the genital corona of *E. forcepopenis* are invariably 12, but only 8–10 are present in *E. micropharyngella.*

5. While both species have a single median vagina with a duct direct to the oötype, in *E. forcepopenis* the vulva is halfway between the male genital pore and the vitelline ducts, and in *E. micropharyngella* it is strikingly farther forward, lying immediately behind the male genital pore.

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 [2] Generic characters are indicated by Arabic numerals, specific characters by small Roman numerals.

6. The relative size of oral pouches (mean diagonal from $\sqrt{l \times w}$) and pharynx in the genotype is 50–77%, the pharynx as usual being ovoid and larger than the ovoid oral pouches. But in *E. micropharyngella,* while the oral pouches are nearly round the ovoid pharynx is minute, the former 130% of the latter. Hence this most obvious specific character is indicated in the name.

In view of these important characters I agree with George (1961) in his creation of *Engraulicola,* with *E. forcepopenis* as the type. The above description was written before the paper by K. C. George was available to me, but we had previously agreed on the nomenclature of his material (described some years earlier than mine) from the same geographical region (South Malabar coast).

Engraulixenus malabaricus gen. et sp. nov.
Figs. 7–11

Several specimens of this new species of engraulid parasite were obtained from the gills of *Thrissocles malabaricus* (Bloch) examined at Trivandrum on July 26, 1955. Four fishes were examined and all were infected by the new parasite as well as by a large number of two different species of Mazocraeidae. Out of the 52 Monogenoidea obtained, 8 specimens belonged to the present species.

This worm is foot-shaped, with a distinct heel and a long slender forebody, the total length being 1.71–2.43 mm and the maximum width 0.45–0.5 mm (Fig. 7).

Mouth subterminal, without especially glandular or muscular lips; oral pouches spherical, 24–28 μ in diameter; pharynx median, very large, elongated ovoid, 64×36 μ–80×38 μ; oral pouches not more than 40% of pharynx (by mean diagonals); oesophagus narrow, 0.13–0.19 mm long, bifurcating into the intestinal crura behind the male genital pore; crura exceptional, with 2–3 cross connections bridging across the median line and without much outer branching, the dilated ends (unbranched in posterior third) extending to different levels. At the anterior region of the long clamp row, the crus of that side has a few wider lateral branches, forming the base of what is probably a metahaptoral wing. An oblique con-
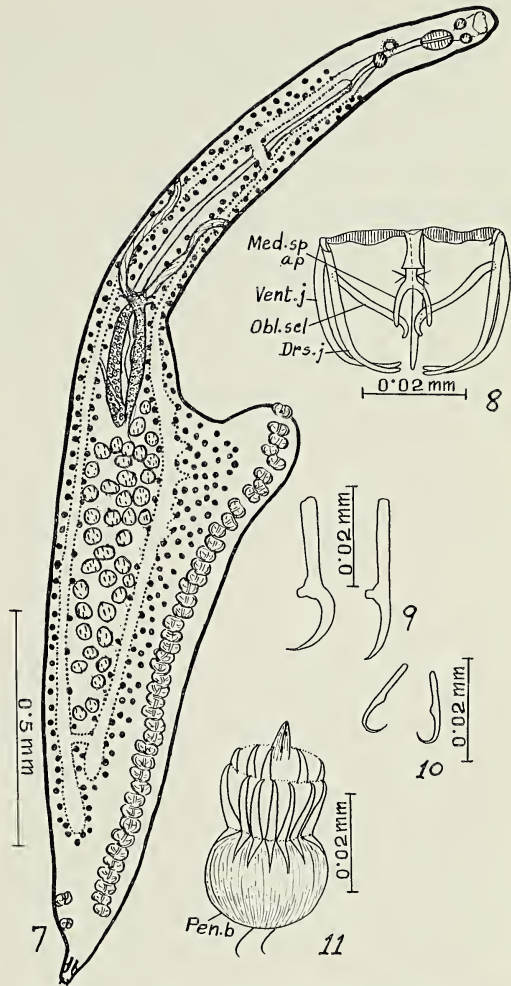
FIGS. 7–11. *Engraulixenus malabaricus* gen. et sp. nov. 7, Complete worm, ventral view; 8, clamp of the long row, dorsal view; 9, proximal anchors; 10, distal anchors; 11, penis with the corona of hooks and forcepiform process.

nection also occurs between the distal ends of the crura, behind the testes zone, in most of the specimens (Fig. 7).

The haptor occupies about 50% of the total length; a fleshy flange adherent to the body (yet with an increasing tendency to diverge from it) forms the wing referred to above. The long clamp row has 42–49 clamps, each 32×48 μ–32×66 μ; the short row has two nearly sessile clamps 24×28 μ, and 28×36 μ; lappet 64×28 μ, armed with two pairs of anchors. The anterior pair (Fig. 9), 32 μ long, have a shape different from that in *Gas-*

trocotyle and *Engraulicola*: the hook is barely a quarter of a circle, with the handle considerably longer, while the stout spur is at right angles to the handle. The posterior anchors (Fig. 10) are also unusual in having an incipient spur behind the short hook; the total length of these anchors is 16 µ.

The clamp structure shows slight variations from that of *Engraulicola*: there is a marked gradation of size toward the middle of the long row. The clamps are much wider than long, except for the first and next anterior clamps, which, like the two remnant primaries of the inhibited side, are more nearly squarish (Fig. 8).

The 20–39 testes are oval, 28 × 40 µ–36 × 48 µ, arranged in 4–5 files in the intercrural field behind the ovary but with a few parovarian testes on the left side. The narrow vas deferens arises from the postovarian testes, extends forward on the left side of the body, parallel to the vitelline duct and enlarges into a seminal vesicle near the anterior end of the median vitelline duct. From the anterior margin of the seminal vesicle, the vas deferens continues forward and opens into the base of the penis, some distance anterior to the intestinal bifurcation. The penis is muscular and armed with a corona of 12 recurved hooks around its bulb-like base, and there is a forceps-like double spine within (Fig. 11). The forceps spines appear rather shorter than in *Engraulicola*. Male genital pore is strengthened by a rim of radial muscle fibres but is without a projecting collar, and is situated at about 0.27 mm from the anterior end of the body.

The inverted ∪-shaped ovary occupies a field in the middle of the body's length and it is about one-tenth as long as the latter, the ova as usual becoming bigger toward the oviduct. The oviduct arises from the distal end of the ovary and enlarges into a small sphincter-like ovijector which continues through the oötype region and opens into the fertilization chamber near the vitelline ampulla. The uterus can be traced forward from the anterior margin of the oötype, parallel to the vas deferens, and it opens into the unarmed uterine pore situated immediately in front of the male pore.

The paired vaginal pores are unarmed and submarginal and lie in front of the ovarian zone at two-thirds the distance from the male

terminalia to the anterior end of the ovary. The vaginal ducts are S-shaped and in the specimens examined were distended with sperm; they run backward and unite in the zone of transverse vitelline ducts to enter the wide median vitelline duct which extends backward, narrows posteriorly, and opens into the oötype, in the small vitelline ampulla. Thus, there is no true median vaginal duct.

The vitellaria extend from the region of intestinal bifurcation to the distal ends of the crura and are not confluent across the median line even in the region of the crural bridges; the spherical follicles are 8–12 µ in diameter. The transverse vitelline ducts meet along with the lateral vaginal ducts immediately *anterior* to the ovarian zone, to form the median vitelline duct which also functions as a vaginal duct. The genito-intestinal canal connects the base of the oötype with the right intestinal crus, passing sharply obliquely forward across the proximal region of the ovary; its union with the right crus is in the midovarian zone (i.e., more anterior than is usual).

RELATIONSHIPS OF *Engraulixenus malabaricus* GEN. ET SP. NOV.:

1. *Engraulixenus* has an elongated tapering body, slender anteriorly, with a long foot-shaped hindbody tapering backward and which has an unusually prominent heel with a spurlike extension; this region is the typical haptoral wing (perhaps a metahaptor: see Unnithan, 1967*b*), which receives short wide branches from the adjacent intestinal crus which branches more or less profusely in the anterior part of the wing; these gut branches carry with them vitelline follicles. The haptor extends slightly obliquely at only 25° to the body axis for at least 50% of its length; thus the zone of pivoting of the attached worm is between the wide testis zone and the ovarian zone. The torque strains set up have not greatly disturbed the symmetry of the body proper but doubtless account for the haptoral wing and subjacent lateral field. The arc of feeding exploration is evidently extensive because of the slender contractile forebody. Thus, *Engraulixenus* is less symmetrical than *Gastrocotyle*.

2. The inhibited clamp row retains two of its primary clamps in all individuals.

i. The long clamp row in mature worms, 1.7–2.4 mm long, bears 42–49 nearly sessile units, closely set, the posterior edge of one touching the anterior edge of the next one.

ii. The larger clamps are at least as wide as long and are the widest of any described in the present study.

iii. The dorsal appendix on the spring is a stalked stout U-shaped piece with parallel arms not divergent as in most of its relatives.

iv. The ventral arm of the spring is not truly bifurcated and is slender throughout.

v. The braces are bent posteriorly for mutual articulation.

3. Of the two pairs of persistent anchors, the anterior are characteristically shaped, with the handle markedly longer than the hook, which is barely one-quarter of a circle, and with a stepped conical spur at a right angle to the handle. The anterior anchors are more slender and shorter than in *Engraulicola*, and the posterior anchors have hooks which recurve for only one-third the length of the blade, and have an incipient spur and a stout handle. They are just half as long as the anterior pair.

4. The forceps on the penis head are similar to those in *Engraulicola*, but they may be relatively stouter and shorter; there is no collar projecting from the rim of the atrium masculinus.

i. The penis spines are sigmoid and 12 in number.

ii. The 20–39 testes are massive in 4–5 files anteriorly.

iii. A vesicula seminalis is present in front of the ovarian zone.

5. In the paired vaginae the vulvae are supramarginal and the lateral vaginae join the transverse vitelline ducts near their confluence, so that there is no true median vaginal duct.

i. The vulvae are situated at two-thirds the distance from the male genital pore to the anterior end of the ovary. The vitelline ducts are usually long and oblique and they become confluent into the median vitelline duct distinctly *anterior* to the ovarian zone.

6. The pharynx is exceptionally elongated and ovoid, the longest (80 μ) in the whole group; the mean diagonal of the spherical oral pouches is 40% or less that of the pharynx.

7. Exceptional intercrural bridges occur twice or thrice in the forebody, and often in the post-testicular zone there is an oblique bridge. This is the most obvious generic feature, but it is perhaps less important than are the preceding criteria taken together.

i. The ends of the crura are subequal and markedly inflated, the longer being on the inhibited side, and reaching to opposite the sixth or seventh clamp from the posterior end.

The specific name is derived from the host and locality, the South Malabar coast.

Engrauliphila grex gen. et sp. nov.
Figs. 12–17

Specimens of this new gastrocotyline genus were found swarming on the gills of *Thrissocles dussumieri* (Val.) examined at the Southern Indian Marine Biological Laboratory at Trivandrum on October 5, 1955 and at Ayirumthengu on September 8, 1955. Those from Trivandrum had a multiple infection including a relative, *Engrauliscobina triaptella* sp. n., while those from Ayiramthengu were infected with the present species only. Numerous specimens were collected from a single fish, a minimum of at least 50 being very common. However, many fishes of the same host species examined at Vizhinjom (another marine biological station, 8 miles south of Trivandrum) on August 19, 1954 were not infected by *E. grex*. There the characteristic parasite was *Engrauliscobina triaptella*.

This worm is foot-shaped with a spurred heel, but the "leg" comprising the anterior half is only about half as wide as the stout hind-body, which tapers evenly to the terminal lappet; total length 1.3–1.8 mm and maximum width 0.25–0.3 mm, including the haptoral wing or spur of the heel (Fig. 12).

The subterminal mouth is wide, with an anterior circlet of scattered sticky cells. The spherical oral pouches are 24–32 μ in diameter, with thin walls but with long muscle fibres extending backward; the relatively long ovoid pharynx is

$40 \times 60 \ \mu$–$44 \times 72 \ \mu$, with thick walls and radial muscle fibres strengthening it; the mean diagonals of the oral pouches are about 50% of the diagonal of the pharynx. The narrow oesophagus is 0.12–0.18 mm long and bifurcates into the intestinal crura just behind the male terminalia. These crura lack both intercrural branches and bridges, and have very few outer

branches; they terminate posteriorly at different levels in the posterior third of the hindbody, where their ends are slightly inflated. The crus on the inhibited side of the haptor is the longer, reaching to opposite the fifth clamp or so from the posterior end of the longer row, well in front of the two clamps of its own side.

The intestinal crus on the side of the body
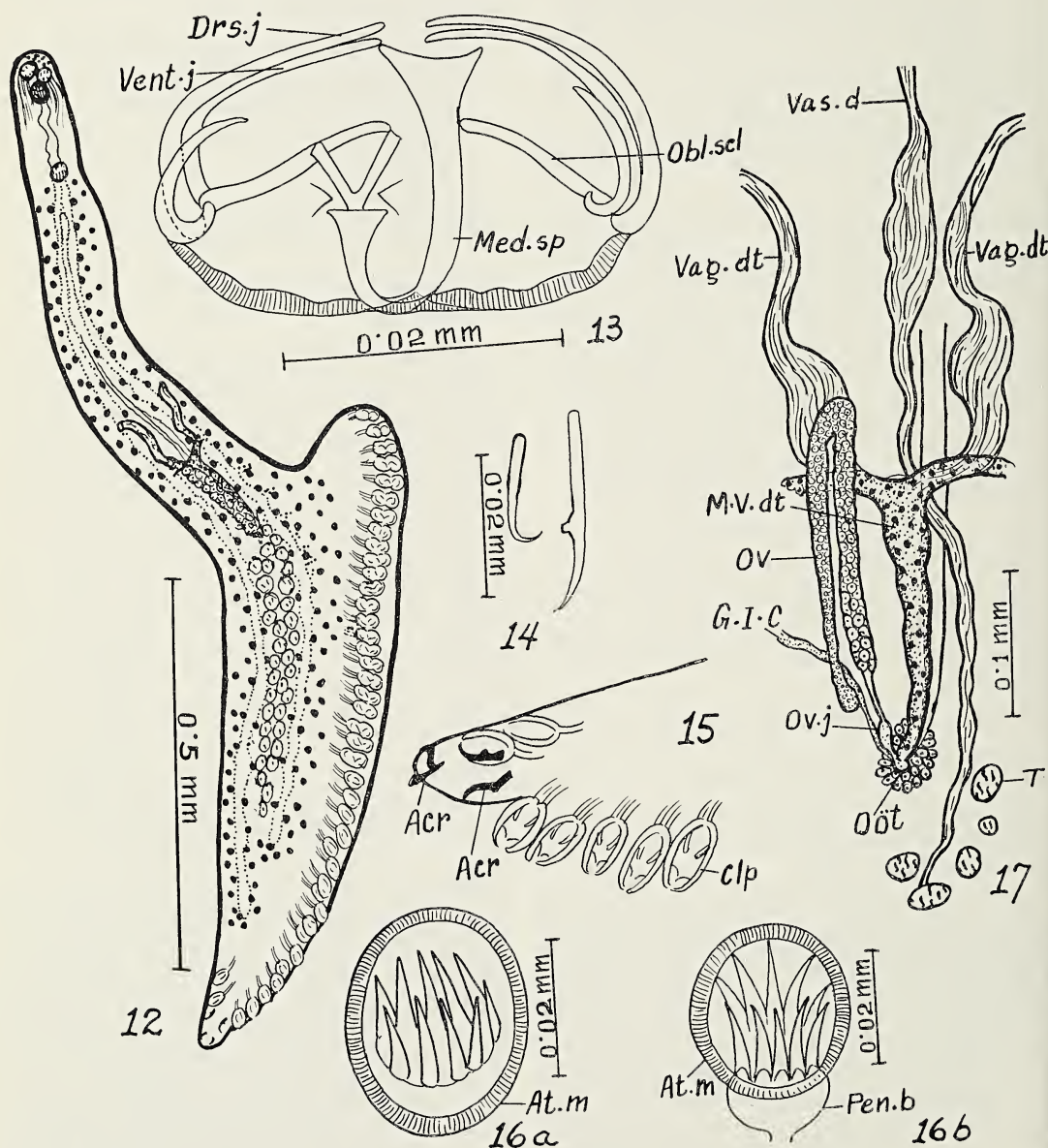
Figs. 12–17. *Engrauliphila grex* gen. et sp. nov. *12*, Complete worm, ventral view; *13*, clamp, ventral view; *14*, anchors; *15*, hind end of haptor with the anchored lappet; *16a* and *16b*, male genital pore with the armed penis; *17*, ootype and ovarian region, ventral view.

bearing the main row of clamps has more extensive outer branches, particularly in the haptoral wing, which are accompanied by vitellaria. This winglike expansion of the haptor is similar to that in *Engraulicola micropharyngella* described above, but although the present worms are on the whole smaller, the haptor is stouter. All the clamps have relatively long muscular stalks (about as long as the width of the clamps) which project sideways in close file. As in the previous species, the clamps increase in size toward the middle of the row, where there is a slight irregularity. This may indicate the end of the euhaptor and the beginning of the metahaptor, which tends to grow with increasing independence of the body proper, its anterior part being free from it—as the metahaptoral wing (Fig. 12). The long row makes an angle of only about 30° with the body axis. There are always two remnant clamps on the inhibited side, smaller (20×28 μ–28×36 μ) and resembling their opposite primaries. The long row is more than half the length of the worm, with 40–48 clamps, each 28×40 μ–28×60 μ.

The terminal lappet is trapezoidal, 0.04×0.02 mm, with two pairs of anchors. The anterior anchors are 28 μ long and slender; the hook is less strongly curved (only one-eighth to a quarter of a circle), with a short stepped spur, projecting at right angles at the end of the slender handle which is more than half the total length (Figs. 14 and 15). Thus there is a strong resemblance to the anterior anchors of *Engraulicola micropharyngella*. The posterior anchors generally resemble those of the last species, but the simple hook is barely one-third as long and is less curved (about half a circle), while in the last species the hook was more than half a circle (cf. Figs. 14 and 10).

The clamp structure is quite distinctive in detail (Fig. 13); the larger clamps are as much as twice as wide as they are long. In sharp contrast to the two previous species, the ventral arm of the median spring is broad and widely bifurcated in a thick pointed fork. The dorsal arm carries a V-shaped stout appendix with arms widely diverging. The braces are not bent at the posterior ends to form articulating facets, as in the preceding species.

The testicular zone is entirely flanked by the haptor flange, which extends over the hind end of the ovary also, so that the pivoting axis is in a thicker part of the worm and the torque here would account for the broad haptoral wing. The testicular zone is not involved in the torque and the 2–4 files are rather regular and compact (Fig. 12). There are 15–31 testes, ovoid or spheroidal, with one or two parovarian testes. The vas deferens is long and wide, arising from the median anterior testicular zone and extending forward as a zigzag duct to open into the base of the penis. The anterior extremity of the vas deferens, before it joins the penis, is straight, forming the ejaculatory duct; this has a posterior dilatation between the horns of the vaginae functioning as the seminal vesicle (Fig. 17); the penis is muscular, ventral, situated about 0.18–0.2 mm from the anterior end, and bearing a corona of 10 sharp hooks, but its tip lacks forceps spines. The atrium masculinus is unarmed and circular, with a muscular rim and a thick ring of radial muscle fibres but no projecting membranous collar (Figs. 16a and 16b).

The ovary takes the form of an inverted $\cup$ with a long narrow proximal (outer) limb and a wide short distal (inner) limb, situated in the middle third of the body, in front of the testicular zone. The thin and narrow oviduct descends from the distal end of the ovary and opens into the fertilization chamber, through the well-developed, spindle-shaped ovijector (Fig. 17). The oötype is surrounded by closely packed Mehlis gland cells. The uterus ascends from the oötype to open into the unarmed uterine pore in front of the atrium masculinus. Eggs were seen in only one of the specimens.

The vitellaria extend from the intestinal bifurcation to almost the distal ends of the crura; they are not confluent across the median line, and their spherical follicles are 8–10 μ in diameter. The transverse vitelline ducts meet to form the median duct at the anterior quarter of the ovarian zone, as in *E. triaptella*, but here they are joined by the lateral vaginal ducts. The median vitelline duct is broad anteriorly and tapers posteriorly to open into the vitelline ampulla, which is feebly demarcated in most of the specimens. The genito-intestinal canal is well differentiated, arising from the oötype close to the ovijector, and running obliquely into the right crus.

The two dorsal vaginal pores are unarmed, one in each midlateral field in front of the ovary in the anterior part of the middle third of the body, well in front of the transverse vitelline ducts. The lateral vaginal ducts are packed with sperm cells and twisted in S-shaped sinuous ducts which run backward to unite with the transverse vitelline ducts near their junction with the median vitelline duct.

RELATIONSHIPS OF *Engrauliphila grex* GEN. ET SP. NOV.:

1. *Engrauliphila* has a haptor-body relation similar to that in *Engraulixenus*.

   i. The stouter body is provided with a somewhat thicker haptoral flange and the clamps have more muscular and longer stalks.

   ii. In comparable-sized worms, the haptor is more extensive, reaching into the ovarian zone, so that the zone of pivoting is in a thicker region and the resulting torque would account for the relatively more massive (metahaptoral) wing.

   iii. The length of the clamp row is more than 50% that of the relaxed worm.

2. The inhibited clamp row retains only two primary clamps in all specimens.

   i. The long clamp row bears 40–48 transversely elongated stalked clamps in close file.

   ii. The dorsal appendix on the spring is stout and V-shaped.

   iii. The ventral arm of the spring is broad, splayed, and bifurcate.

   iv. The braces do not have bent articular ends.

3. The two pairs of persistent anchors are of distinctive shape, both less curved than in *Engraulixenus* and entirely unlike those of *Gastrocotyle* and *Engraulicola*.

4. The penis head is devoid of forceps and a collar is lacking round the atrium.

   i. The corona consists of 10 sharp divergent spines, but no sigmoid spines.

   ii. The 15–31 testes are in 2–4 compact files, with 1 or 2 parovarial.

   iii. There is a vesicula seminalis in the pre-ovarian zone.

5. The vaginae are paired and lie in midlateral fields on the dorsal side; there is no median vaginal duct, since they join the transverse vitelline ducts near their confluence, as in *Engrauliphila*; the vulvae are not supramarginal and are situated much nearer the ovary.

   i. The vulvae are less than an ovary length in front of the ovarian zone.

   ii. The transverse vitelline ducts are situated at the level of the anterior quarter of the ovarian zone.

6. The pharynx is elongated ovoid, and the oral pouches are spheroidal and much smaller.

   i. The mean diagonal of the latter is about 50% that of the pharynx.

   ii. The crura lack inner branches and there are no intercrural bridges at all.

   iii. The unequal ends of the crura are only slightly dilated.

The assemblage of differences in the generic criteria taken together are in sufficient contrast to those of *Engrauliphila* for *Engraulixenus* to be recognized as distinct. The specific name *grex* refers to the exceptionally high infestation rate on *Thrissocles dussumieri*.

Engrauliscobina triaptella sp. nov.
Figs. 18–25

Specimens of this second species of *Engrauliscobina* Unnithan, 1967b were obtained from the gills of *Thrissocles dussumieri* (Val.) examined at Vizhinjom and Trivandrum on August 19, 1954 and October 5, 1955, respectively. Two fishes examined at Vizhinjom were infected by four individuals (two on each fish), while several of the *T. dussumieri* examined at Trivandrum were found to be parasitized by one specimen of *E. triaptella* along with a large number of *Engrauliphila grex*. Such multiple infection was not observed on the several *Thrissocles dussumieri* examined at Ayiramthengu on September 8, 1955, which were infected only by *Engrauliphila grex*.

The essential asymmetry of these worms is shown typically in one of the longer but somewhat contracted specimens (Fig. 18); a younger one is shown extended in Figure 19, in which the bulging of the shorter side is marked. The characteristic shape is triangular, as it is in the

genotype *Engrauliscobina thrissocles* (Tripathi). There is no demarcation of the haptoral region from the body proper, since the clamp row flanks the side of the body opposite the anterior region of the testicular zone or extends partly into the ovarian zone providing one of the shorter sides of the triangle. The length of these typical specimens is 2.4 and 2.9 mm, and their maximum width (between the gonad zones but excluding the haptoral wing) is 0.4 and 0.7 mm, respectively, giving a width-to-length ratio of 16.5%:24%—the latter being more typical. The worms are strongly flattened dorsoventrally and highly extensible and contractile; in extension they are able to flex the body over a wide arc based on the fixed haptor, the axis of pivoting being in the thickest and widest

zone; the resulting stresses would account for the convexity on the short side above the long clamp row. The shape of the whole body is like that of a scraper (particularly so in the genotype); the handle of the scraper is here more abruptly demarcated, forming the neck which is about one-fifth the total length of the body axis, as it is in the genotype; and here again the body axis is bent at a small angle between the ovarian and testicular zones, even in the contracted specimen (cf. my Fig. 18 and Tripathi's [1959] Fig. 56a).

The subterminal mouth has scattered gland cells only on the anterior lip. The oral pouches are longitudinally ovoid, 24 × 20 μ, and have long muscle fibres extending posteriorly from their thick outer walls. The pharynx is oval,
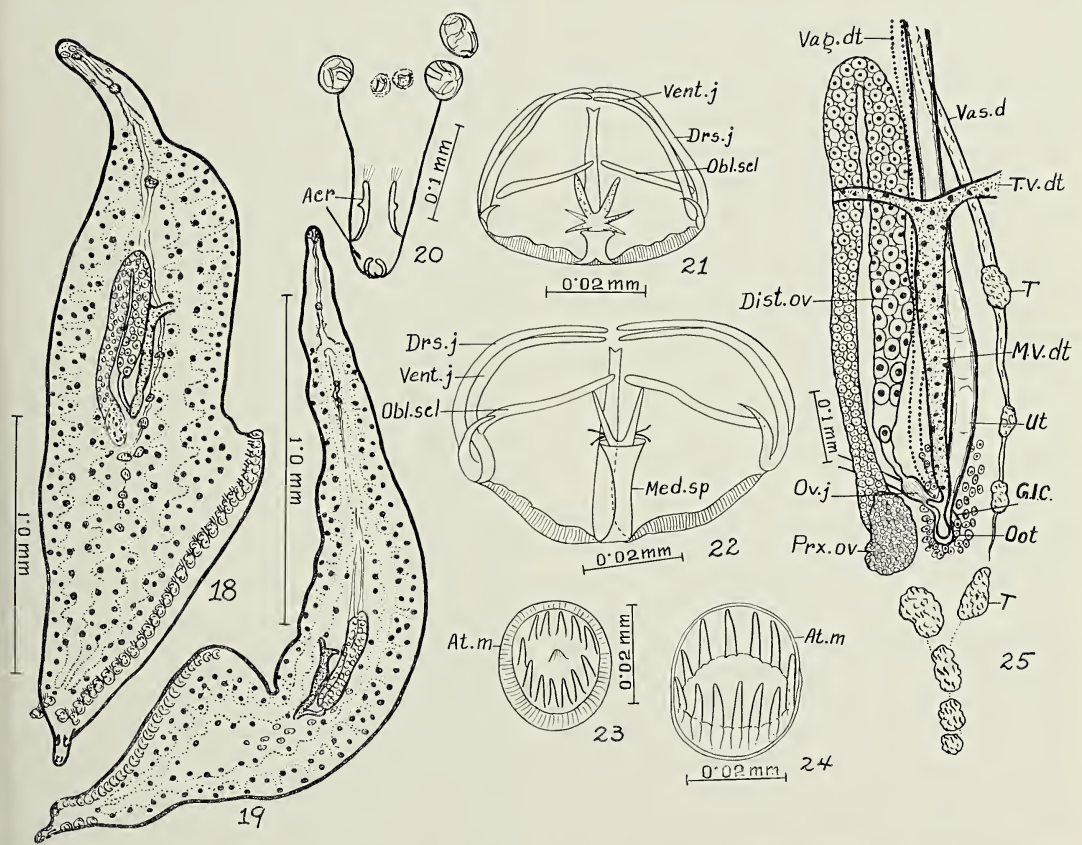
FIGS. 18–25. *Engrauliscobina triaptella* sp. nov. *18,* Complete worm, ventral view; *19,* another complete worm with three clamps in the short row; *20,* hind end of the haptor with the pair of incipient clamps of the worm with only two clamps in the short row; *21,* first clamp nearest the lappet on the short row, dorsal view; *22,* one of the middle clamps of the long row, dorsal view; *23,* male genital pore with the penis head; *24,* corona of spines of the male genital pore; *25,* oötype and ovarian region, ventral view.

thick-walled, and only slightly larger than the oral pouches, 24 × 40 μ, the mean diagonals of the pouches being as much as 70% that of the pharynx. The oesophagus is 0.16 mm long and unbranched, and bifurcates into the intestinal crura immediately behind the male genital pore. At the posterior end of the neck region, the crura have numerous complex outer branches and a few simple inner branches; they are particularly extensive on the side bearing the clamp row. The crural ends are close together near the tip of the body, but they are not confluent across the median line, nor were any intercrural bridges seen.

The haptor, represented by the unilateral clamp-bearing flange on the hindbody and including the lappet, is slightly less than half the total length of the slightly contracted worm (Fig. 18), but in the extended condition it is only 36%. The long clamp row (usually on the left) is 0.825–1.35 mm long, bearing 27–35 almost sessile clamps. The inhibited side of the haptor is represented in all specimens by 3 remnant clamps, and together they make a row only 0.10–0.12 mm long. Occasionally (as shown in Fig. 18), there may appear to be only 2 remnant clamps in the short row (usually the right side in my collections), but in Figure 20 it will be seen that the first two primary clamps are relatively minute and lie close together near the median line between the second pair of primary clamps—virtually the end clamp of each row. In most specimens the three clamps of the inhibited side are subequal and in a linear series, as in Figure 19.

The terminal lappet is short, narrow, and cylindrical, 0.82 × 0.25 mm–0.98 × 0.48 mm, armed with two pairs of symmetrically arranged anchors. The anterior anchors have their hooks only slightly sickle-shaped (one-quarter to one-third of a circle), with a knoblike spur at the top of the slender handle, which may be less than one-half the total length of the anchors (40 μ). The posterior anchors are almost ⊂-shaped, with a reflexed strongly rounded hook but a very short handle (total length 12–16 μ). Both pairs of anchors are similar to those figured by Tripathi (1959), but while the anterior pair is like those of *Engrauliphila* the posterior pair resembles only those of *Engraulicola micropharyngella*.

The clamps in the long row are 44 × 52 μ–35 × 75 μ, and in the short row 20 × 28 μ–30 × 48 μ. Thus, the primary clamps of both rows are smaller and only slightly wider than long, but those in the long row are graded as usual, the largest being on either side of the middle region, and more than twice as wide as long. The braces are situated across this longer diameter; they are nearly straight with bent ends lacking the bent articular facet, though they do meet medially near the level of the divergent V-like arms of the dorsal appendix. The ventral arm of the spring is very slender, with or without a very slight enlargement at its end, but this extremity is always with a minute notch, never truly bifurcated (see Figs. 21 and 22).

There are 9–12 irregularly oval testes, 60 × 75 μ–75 × 150 μ, arranged in two files and not in a single mass as depicted for the genotype. The row on the side opposite the clamps is completely postovarian, while that nearer the clamp row extends forward to the middle of the ovary along the outer edge of the median vitelline duct; these parovarian follicles were not found in *E. thrissocles*. The vas deferens originates from the anteriormost testes of the parovarian file, runs forward parallel to the uterus, and opens into a zigzag ejaculatory duct which in turn opens into the penis. No vesicula seminalis was seen. The muscular penis is small and conical, without forceps, and opens into the circular atrium masculinus, which is surrounded by a muscular ring 20–24 μ in diameter, situated at about 0.16–0.19 mm from the anterior end of the body. The penis itself bears around its widest diameter a corona of 12 sharp conical spines pointing vertically from the ventral surface; the spines are nearly straight. Figures 23 and 24, drawn from ventral and dorsal aspects, are intended to demonstrate the entire absence of forceps on the penis head.

The ovary is in the form of an elongated inverted ∪, with the distal (inner) arm wider and containing a number of large ova, and the proximal end slightly swollen and overlapped by the anterior testes of the postovarian file. The short and narrow oviduct expands slightly to form a muscular ovijector, before opening into the vitelline ampulla (Fig. 25). The wide median uterus arises from the outer margin of the fertilization chamber in the oötype, runs

forward parallel to the common vitelline duct, and opens into the unarmed uterine pore in front of the male genital pore. Two or three eggs with polar filaments were observed in most of the specimens, but usually were too collapsed for reliable measurements.

The vitellaria occupy wide lateral fields extending from the zone of intestinal bifurcation to the hind end of each crus; follicles are spherical, 20–25 μ in diameter, not confluent across the median line. The transverse vitelline ducts are broad and lie at the level of the anterior quarter of the ovary; the median vitelline duct is long and wide, and originates behind the anterior third of the ovary; it narrows as it passes backward, and it opens into the swollen vitelline ampulla in the oötype region (Fig. 25).

The single median dorsal vaginal pore is circular, 20 μ in diameter, unarmed, but surrounded by a group of small spherical gland cells. It is situated a short distance behind the intestinal bifurcation (midway between the male genital pore and the transverse vitelline ducts). It is in this zone that asymmetry is particularly striking: on the side of the clamp row (usually at the left) there is, at least in nonextended worms, a marked hump on the profile before the indentation at the base of the neck (Fig. 18), and a low furrow from the vulva on the dorsal side leads obliquely to the indentation. This is the anterior limit of the lateral branching of the crus and attendant vitellaria of that side. On the opposite side the profile is nearly straight from the neck zone to the lappet, and the vitellaria extend farther anteriorly along with short external crural branches to the bifurcation on that side. This notch opposite the vulva may facilitate a finer hold during copulation in these worms, where the torque from the oblique attachment must be considerable. The median narrow vaginal duct runs backward dorsal to the uterus, between the oviduct and the median vitelline duct, to open directly into the fertilization chamber. It is quite independent of the vitelline duct. The genito-intestinal canal originates from the base of the oötype, runs parallel to the ovijector, and opens into the intestinal crus.

Two ill-defined excretory pores, one on each margin, are noticeable, midway between the male genital pore and the pharynx.

RELATIONSHIPS OF *Engrauliscobina triaptella* SP. NOV.:

1. In the more or less contracted state, *E. triaptella* is a triangle with the long clamp row as its shortest side; the inhibited haptor side of the worm is only slightly convex. In the generally similar genotype, *E. thrissocles* (Tripathi, 1959), the body is a much narrower triangle; in both there is a narrow neck, about one-fifth of the total length. The haptoral row embraces more of the body in the genotype, including the hind region of the ovarian zone, but it is more restricted in *E. triaptella,* being barely included in the ovarian zone. Hence, the torque in the latter species is less, and the (meta-) haptoral wing is not so extensive, in order to balance these stresses, as it is in the genotype. A further consequence of the torque is visible in *E. triaptella* in the vaginal zone, marked by a hump on the profile on the attached side of the worm and an inhibition of lateral crural branches and vitellaria anterior to the hump and neckbase, the opposite side being unaffected. In fact, the asymmetry in this species is more marked than in any other gastrocotylid and approaches that in some Opisthogynidae and Protomicrocotylidae.

    i. The clamp flange is about 36%–48% of the total length in *E. triaptella* (the greater the contraction the greater the proportion, of course), while in the genotype it is about 50%.

    ii. The angle made by the haptoral axis with that of the body proper is about 45°, compared with nearly 60° in the genotype.

    iii. The body torque produces a permanent slight bend in the axis of the ovarian to the testicular zones.

2. There are remnant clamps on the inhibited side of the haptor, only 2 in the genotype, but 3 in *E. triaptella* (hence its name). The uninhibited row in mature worms bears at least 30 nearly sessile clamps.

    i. There are up to 35 clamps in the new species, but 40–42 in *E. thrissocles.*

    ii. The secondary clamps (but not the squarish primaries) are at least twice as wide as long in *E. triaptella.*

    iii. The ventral arm of the median spring is

slender and tapers to a minutely notched tip.

iv. The dorsal appendix on the spring is a simple V shape.

v. The braces are slender and nearly straight and lack the bent articular distal facet in *E. triaptella*. There is no description or figure of the secondary clamps for *E. thrissocles*.

3. The two pairs of persistent anchors on the lappet are of characteristic shape in both species. The genotype retains a pair of minute larval hooks at the tip of the lappet.

i. The anterior anchors are slender, with feebly curved hooks (about one-third to one-half a circle), and with a knoblike spur and the handle barely half or less of the total length (40 μ).

ii. The posterior anchors are ⊂-shaped or sharply reflexed simple hooks with negligible handles (root).

4. The penis head is absolutely devoid of forceps, the corona hooks are straight.

i. There are 10 penis hooks in *E. triaptella* but 12 in *E. thrissocles*.

ii. There are 9 to 12 irregularly shaped, rather large testes in two files, with some of the files (nearer the clamps) parovarial. In *E. thrissocles* there are perhaps no parovarial testes.

iii. There is no intercalary vesicula seminalis on the vas deferens.

5. The single median dorsal vagina leads to a median duct independent of the vitelline ducts.

i. The zone of the vulva is midway between the male genital pore and the ovary.

ii. The vitelline ducts are horizontally transverse at the first quarter of the ovarian zone.

6. The moderately ovoid pharynx is only about twice as long as the oral pouches.

i. The oral pouches' mean diameter is about 70% of that of the pharynx (about 56% in the genotype).

ii. The lateral crural branches are extensive in the haptoral wing, but there are no intercrural bridges and the crura extend without dilation to near the posterior tip of the body in both species.

The two species are closely related yet clearly distinct and occur on different species of *Thrissocles*, the genotype occurring in the northern Bay of Bengal (Puri) and *E. triaptella* in the South Arabian Sea and at two stations in southern Kerala.

Pellonicola elongata gen. et sp. nov.
Figs. 26–33

Several specimens of this new gastrocotyline were obtained from the gills of *Pellona (Ilisha) brachysoma* (Blkr.) examined at Trivandrum in 1955. A single fish 17 cm long was examined on July 5, and 4 parasites were found on its outer gills; a single female fish 17 cm long, examined on August 27, had 4 parasites. From 5 fishes 18 cm in average length, examined on July 27, 14 specimens were obtained. The 4 specimens collected on July 5 proved to be the longest among the total of 22 specimens.

The long, narrow, ribbon-like body (2.25–4.5 mm long, maximum width 0.25–0.48 mm, or one-tenth its total length), tapers gently forward to a nearly straight neck little more than one-tenth of the total length and itself one-fifth to one-quarter as long as wide. The middle third of the body is expanded 25% to accommodate the ovarian zone and reaches its maximum at the proximal ovarian zone; behind this the testicular zone is almost straight-edged and is as wide as the preovarian zone (Fig. 26). The haptor is relatively far shorter than in any other gastrocotyline yet known, barely one-fifth the total length (0.525 × 0.15 mm–1.0 × 0.3 mm), one clamp row being twice as long as the other, with subsequal clamps ending in a short telescopic lappet.

The subterminal funnel-shaped mouth is surrounded by a highly muscular spherical-to-oval organ having a deep circular lip with a ventral notch, and a chamber measuring 45–50 μ. Behind it are the ovoid oral pouches, 20 × 28 μ–24 × 36 μ, and these have thick walls and long muscle fibres extending down the length of the neck (Fig. 27). The pharynx is a large ovoid structure, 34 × 38 μ–36 × 40 μ. The mean diagonal of the oral pouches is about 61–78%
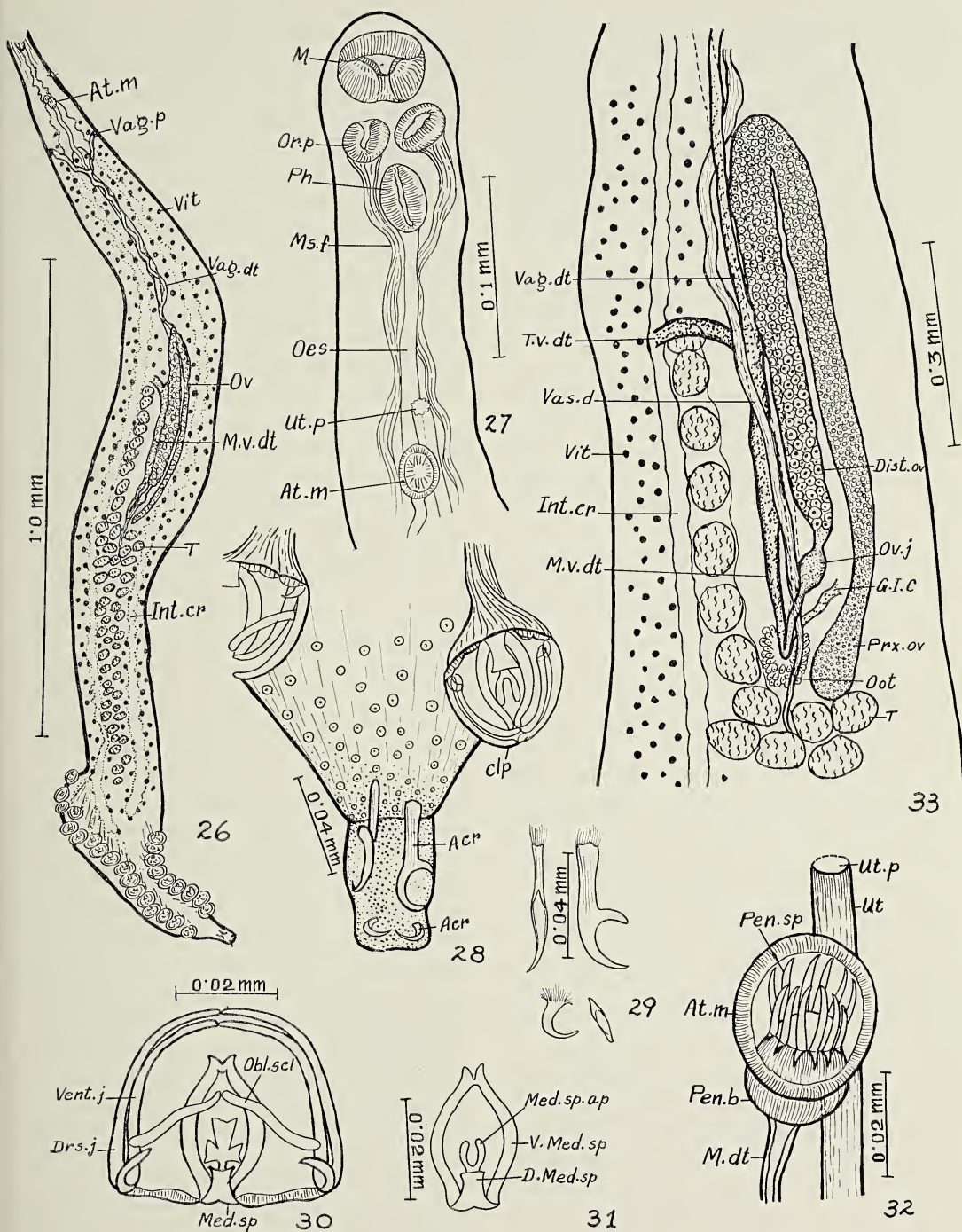
FIGS. 26–33. *Pellonicola elongata* gen. et sp. nov. 26, Complete worm, dorsal view; 27, anterior region, dorsal view; 28, terminal lappet with anchors; 29, anchors; 30, clamp, dorsal view; 31, median spring of the clamp of another worm, dorsal view; 32, male terminalia with the uterus, ventral view; 33, middle of the body, dorsal view.

of that of the pharynx. The oesophagus is long, narrow, and unbranched, and bifurcates into the intestinal crura well behind the male pore. The crura have relatively few regular outer branches, extend backward to the level of the proximal end of the short row of clamps, and terminate independently, but close to each other, without inflations. The crus adjacent to the longer clamp row sends out wide oblique branches to each of the anterior clamps.

The haptor in *Pellonicola*, in contrast to that in all the previous genera, is distinct from the body proper and constitutes a posterior tail. Its right and left haptoral frills are parallel, but one is only half as long as the other: in my specimens, the left frill is always the longer, 0.45–0.93 mm; the right frill range is 0.225–0.456 mm and it bears 8–10 clamps, 36 × 20 μ–44 × 36 μ, while the left frill has 17–22 clamps, 36 × 24 μ–48 ×32 μ.

The terminal lappet apparently is unique in its telescopic arrangement and consists of an oblique plaque capable of being retracted as a whole into the hollow end of the haptor (Fig. 28); it is 60 × 28 μ–68 × 36 μ, and is armed with the usual two pairs of anchors (Figs. 28 and 29). The anterior pair is distinctively shaped like a sickle, 40–44 μ long, with the handle about equal in length to the hook, but the spur root is more than half as long as the handle and projects at right angles from it. The tip of the spur is slightly curved but does not actually pivot backward, as in *Engraulicola micropharyngella* (Fig. 3), which otherwise it most resembles in this series (particularly on account of its sickle hook, which is slightly more than a half circle, although the handle is more slender and relatively longer). The posterior anchors are bent in a deep ⊂-shape and their over-all length is only 16–20 μ with virtually no handle, as in *Engrauliscobina triaptella* (Fig. 20, compare with Fig. 29). The placing of the anchors is invariable; the anterior pair is always directed outward and the posterior pair inward, their hooks nearly touching, in all genera.

The clamps are, exceptionally, slightly longer than wide, but their structure is very different in detail from any of those previously discribed: the median spring is highly modified, the ventral arm being vase-shaped in outline and ap-

parently split longitudinally, with each half bowed outward; the tip is bifurcated. The short arm of the median spring, which has radiating tendonous striae at its distal end, has an appendix which in some specimens is typically ∪-shaped (Fig. 31), but in others is shaped like half a Maltese cross (Fig. 30). The braces (oblique sclerites) are stout and slightly wavy, and, although their inner ends touch in the middle line, there is no sharp bend here to form the familiar articular facet. The dorsal arm of the ventral jaw sclerite is unusually small, often appearing as a mere knob at the region of articulation of the dorsal and ventral jaws (compare Figs. 28 and 30).

There are 34–52 testes arranged in 2–3 rather regular files. On the side of the uninhibited clamp row there is a single file of a few testes extending parovarially up to the level of the transverse vitelline duct on the left side (Fig. 33); the anterior testes are largest (48 × 68 μ), while the posterior ones are smaller (16 × 20 μ). The vas deferens is long and zigzag, arising from between the anterior testes and running forward; in front of the ovary it widens into a large vesicular duct to about the level of the lateral vaginae, behind the intestinal bifurcation. This part probably functions as a seminal vesicle. Thence the vas deferens continues forward, to open into the base of the penis. The muscular cuplike penis is armed equatorially with a corona of 10–12 recurved spines, 10–12 μ long (Fig. 32), but the penis head within is devoid of forceps. The median ventral atrium masculinus has a rim of radial muscle fibres and is situated at about 0.12–0.27 mm from the anterior end of the body, in front of the intestinal bifurcation.

As usual, the ovary is in the form of an inverted ∪ and is situated in the middle third of the body, slightly shifted to the right side; the proximal region is oval and lies immediately in front of the testicular zone on the right side; it is long and narrow, and the distal limb is short (two-thirds the length of the longer limb) and contains large ova, each 12–14 μ in diameter. The short and narrow oviduct descends from the distal end of the ovary and enlarges into a well-demarcated ovijector at about the middle of its length and thence continues backward to open into the median vitelline duct,

within the oötype region (Fig. 33). The wide median uterus, with cuticularized walls, ascends from the distal margin of the oötype, extends forward beyond the vaginal region, and opens into the unarmed, ventral, uterine pore, immediately in front of the male pore (atrium masculinus) (Fig. 32). In one of the specimens a collapsed egg, with a body 120 μ long, was observed at about the middle of the uterus.

The vitellaria extend from behind the zone of the male terminalia to the anterior level of the short row of clamps, surrounding the crura and their branches but not confluent across the median line at the hind end; the vitelline follicles are spherical, 14–16 μ in diameter. The transverse vitelline ducts are slightly oblique and are situated near the posterior end of the anterior third of the ovarian zone; at their confluence they receive the median vaginal canal. The median vitelline duct extends backward parallel to the ovary and opens into the vitelline ampulla. The genito-intestinal canal is very narrow, irregularly wavy, and arises from the oötype. It runs obliquely forward to open into the right intestinal crus, near the proximal limb of the ovary.

The vaginal pores are unarmed, just supramarginal on each side of the body at about 0.25–0.52 mm from the anterior end, with the right pore usually slightly anterior to the left. The two vaginal ducts from the base of the lateral vaginal pores unite obliquely as a V across the median line to form a long median zigzag vaginal duct which runs backward, dorsal to the uterus, and opens into the median vitelline duct at the junction of the transverse vitelline ducts, hence *indirectly* to the oötype region. In most of the specimens traces of vitelline matter were observed extending forward beyond the level of transverse vitelline ducts, into the median vaginal duct. Spindle-shaped eggs, with a filament at each pole, were seen in worms 4.5 mm long.

RELATIONSHIPS OF *Pellonicola elongata* GEN. ET SP. NOV.:

1. The elongated ribbon-like body with the distinct but short caudal haptor is outstanding in Gastrocotylinae. The body proper is free from the attachment zone, so the zone of pivoting in the extreme feeding attitudes is behind

the testicular zone; but, because of the inequality of the attachment basis, the stresses will be slightly greater on one side than on the other, and so the profile in contracted worms is not as symmetrical as in *Microcotyle*, for instance. This slight asymmetry is most obvious in the vaginal zone at the neckbase, as it is in the most asymmetrical species of *Engrauliscobina*.

   i. The body axis makes an angle of up to 60° with the haptor axis.

   ii. The ratio of body width to length is only 1:10, and of haptor to body length about 1:5.

2. The unilateral inhibition is far less than that in any other genus of the asymmetrical gastrocotylines. In this respect it is comparable with *Scomberocotyle* Hargis, 1956, but in that genus a metahaptoral wing, or a secondary stimulation of the secondary clamp replication, accounts for the larger number of clamps on one side (Unnithan, 1967b). It is possible that further observation on *P. elongata* may show that a similar growth relation exists here and that the anterior moiety of the long clamp row does represent a metahaptor, the posterior moiety being the euhaptor with regular paired clamps in the opposite row. If this is so, the formative region for the long row would be near its middle, and that of the short row at its anterior limit, as is usual for the euhaptor.

   i. The long row has a total of 17–22 clamps, while the shorter has 8–10.

   ii. All clamps are slightly longer than wide. Perhaps this is a generic character.

   iii. The ventral arm of the median spring is of a unique vase shape and is split and bowed, joining distally in a very short bifurcation.

   iv. The appendix on the short dorsal arm is sometimes cruciform, indicating an incipient cuticularization of the lateral ligaments.

   v. The dorsal arms of the ventral jaw rami are remarkably reduced.

   vi. The braces across the middle of the capsule are stout but lack distally bent articular facets.

3. Two pairs of persistent anchors are present on a telescopic lappet. Anterior anchors are

sickle-shaped, at least half a circle, with a nearly equal handle and a curved (not bent) spur.

    i. Anterior anchors 40–44 μ, posterior anchors 16–20 μ bent in a deep ⊂-shape.

4. No additional sclerites are formed within the penis corona.

    i. 10–12 curved penis hooks, and atrium well in front of intestinal bifurcation.

    ii. 34–52 testes in 3 compact files with 6–8 parovarian testes.

    iii. Intercalary vesicula seminalis anterior to ovarian zone.

5. There are two paired lateral vaginae with the vulvae supramarginal, as they are in *Engraulixenus*, but very far forward (one-fifth of distance from male pore to anterior border of ovary). The lateral ducts run obliquely back in a Y, to form a median vaginal duct (unusual with paired vaginae) which does not run directly to the oötype, but is confluent with the median vitelline duct.

    i. The horizontal transverse vitelline ducts are at the level of the mid third of the ovarian zone, which is rather more posterior than in related species.

6. The ovoid pharynx is not particularly long (as it is in *Engraulixenus* and *Engrauliphila*), but the oral pouches are more powerful than in other genera.

    i. The mean diagonal of the oral pouches is 66–78% of that of the pharynx in *P. elongata*.

    ii. There are distinct simple branches of the right crus to each of the more anterior (unpaired) clamps of the long row.

    iii. The crura are nearly equal and extend to the body tip without dilatations.

7. There are no intercrural bridges, but there is an exceptional circumoral, sucker-like, circular lip in *Pellonicola* that is not present in allied genera.

The above characters show that *Pellonicola* is a somewhat aberrant gastrocotyline, and that it is the first ever found on a member of the Clupeidae.

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The Growth of *Arachnoides placenta* (L.) (Echinoidea)

Judith Hines and Ron Kenny[1]

ABSTRACT: *Arachnoides placenta* (L.) increases in diameter 7 mm during the first year, 4 mm during the second year, and 4 mm in the third year after metamorphosis.

The relationship between diameter and weight of the test is approximately of cubic form.

The spawning period in north Queensland probably is June to July, and the time of metamorphosis probably September.

The growth characteristics are compared with other echinoid species.

THE "SAND DOLLAR," *Arachnoides placenta* (L.), has been recorded from a wide geographical area ranging from the Andaman Islands through the Philippines and along the northern and northeastern coasts of Australia (Clark, 1946). The distribution of the species on the Queensland coast extends from Thursday Island (Clark, 1921) to Mackay (Endean, 1953, 1956). Clark (1938) recorded some observations on the habits of this "sand dollar" from Darwin, but no data on the growth of the species have been traced.

METHODS AND RESULTS

The animals used in this study were taken at Lucinda (18°31′S, 146°19′E) in the middle of the range of *A. placenta* along the Queensland coast. Lucinda beach is a gently sloping sandy strand with many offshore shoals. The spring tidal range is 8 ft. At low tide *Arachnoides* is distributed from approximately mean sea level to below low water of spring tides, lying on, or a little under, the sand surface.

Collections were made at daytime spring low tides on 10 occasions from March 1961 to February 1962. In collecting, all specimens within a narrow strip extending from the last high water mark to below low tide were taken. In general, animals were collected by hand, but random digging and sieving along the length

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of the traverse ensured sampling of the population down to a diameter of approximately 6 mm.

Measurements of diameter were read to the nearest millimeter and weights of oven-dried whole animals to the nearest milligram.

The temperature data were recorded at Townsville Harbour breakwater (19° 15′S, 146° 50′E) and varied from a June mean of 20.5°C to a January mean of 31.5°C (Fig. 3).

The records of diameters were arranged in 1-mm class intervals (Table 1), and the data were smoothed prior to plotting as a series of monthly histograms (Fig. 2). From these histograms the modes of frequency distribution of diameter were extracted and drawn as a growth curve (Fig. 3).

These results show *Arachnoides* increasing in diameter from 11 to 18 mm during the November to February period of the first year after metamorphosis. From March to October there is little increase in size, but a second season of active growth commences in October and in the ensuing three to four months the diameter enlarges from 18 to 22 mm. In the second year there is a further seven- to eight-month period with no obvious growth, followed by another growing season when the animal increases from 22 to 26 mm in diameter during approximately four months.

The rate of growth during the active growing period decreases with age, being 2.3 mm per month in the first growing season, 2 mm per month in the second, and 1.3 mm per month in the third.

FIG. 1. Selected examples of *A. placenta*.

The period of growth occurs during the part of the year when sea water temperatures are rising (Fig. 3).

The relationship between diameter and weight of test for 125 selected specimens is shown in Figure 4. The equation for the relationship is of the form

$$\log W = 3.061 (\log d) - 1.519$$

where *W* is the weight of the dried test and *d* the diameter of the animal.

DISCUSSION

Extrapolation from the known data would suggest that metamorphosis occurs during September. If it is assumed that the length of larval life is similar to that for another tropical echinoid, *Tripneustes esculentus*, which is two months (Lewis, 1958), it may be deduced that *Arachnoides placenta* spawns in June or July. Lewis (1958) lists July and August as the spawning period for *T. esculentus;* and Hyman (1955), quoting Mortenson, notes that *Mellita*

sexiesperforata spawns in March and April in the West Indies. It would appear that the West Indian species spawn during the early summer for their locality, while *A. placenta* spawns during the Queensland winter at sea temperatures between 20°C and 22°C.

The occurrence of some *Arachnoides* individuals of diameters up to 36 mm suggests a life span of up to five years, assuming the rate of growth for older animals to be similar to that calculated for specimens up to the third year. Crozier (1920) suggested four to five years as the normal life span for the similar but larger Atlantic species *Mellita sexiesperforata* at Bermuda, and Moore (1934) estimated four to eight years as the duration of life for *Echinus esculentus* in Britain. Lewis (1958), working with *Tripneustes* at Barbados, was not able to determine a life span because of commercial fishing for the species.

The recording of a specimen of *A. placenta* of 96 mm diameter from Lindeman Island (Clark, 1946) suggests the possibility of a situation similar to that described by Moore

TABLE 1

Frequency Distribution of Diameter in Millimeters of *A. placenta* (Original Data)

DIAMETER (IN MM)	NUMBER OF SPECIMENS										
	MAR. 25	MAY 21	JUNE 15	JULY 17	AUG. 15	OCT. 5	CCT. 22	NOV. 21	DEC. 12	JAN. 16	FEB. 12
7						5					
8				1	1	1					7
9				4		1					1
10	1	1		2	2	3					3
11	1	1		11	7	5	1	1			7
12	1	1	4	11	8	8		1			2
13	6	3	6	25	13	15	1				6
14	3	9	2	33	15	25					4
15	10	10	8	51	30	35	3			7	6
16	2	13	5	60	35	31	3	1	3	13	10
17	17	17	10	65	60	36	6	10	2	12	9
18	26	22	30	63	55	40	8	20	9	29	22
19	34	22	25	55	45	27	21	24	20	33	25
20	33	22	30	43	68	27	23	53	37	24	11
21	35	22	31	45	38	16	33	50	50	31	19
22	41	25	24	47	36	12	35	45	49	28	24
23	31	26	29	33	24	11	31	43	45	25	17
24	33	23	18	34	24	13	22	24	45	18	10
25	26	25	14	47	15	9	21	25	28	14	24
26	21	17	11	34	13	4	11	20	11	26	23
27	8	15	10	20	9	2	11	11	14	23	9
28	17	15	16	14	6	5	10	13	12	8	5
29	7	10	16	13	10	2	7	7	12	5	4
30	4	6	5	5	2	2	2	2	4	2	3
31	3	4	1	2	1	4	2	1	1	4	3
32		6	5	2	2		4	3	2	3	4
33	2	1	5	4	2		1			2	3
34						1		1	1	1	2
35			1			1		1			
36			2		1						
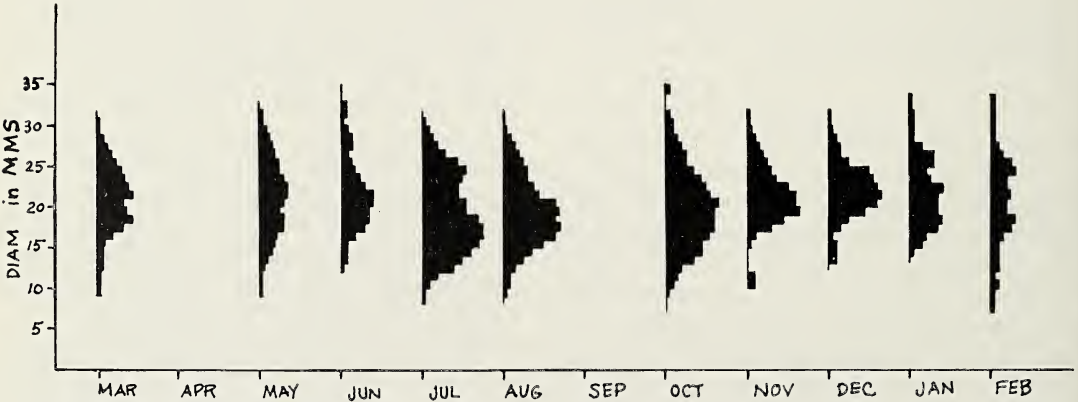
Fig. 2. Frequency distribution histograms of diameter in millimeters, *A. placenta* (smoothed data).
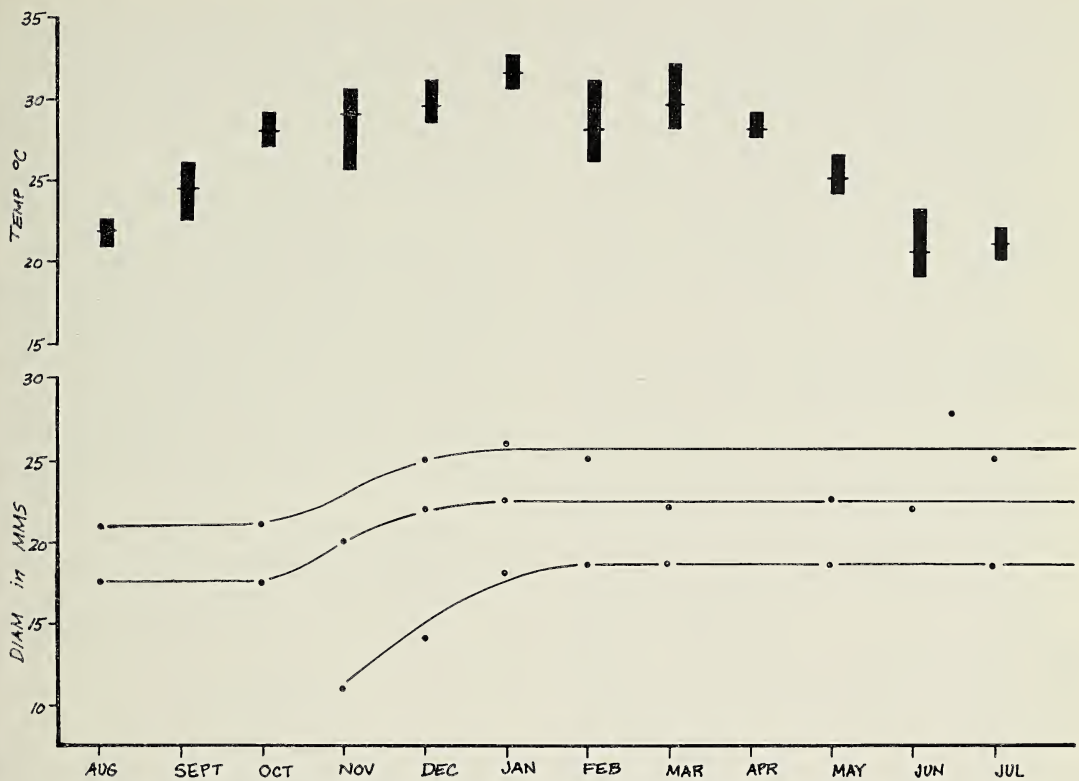
FIG. 3. Growth curve for *A. placenta* related to sea water temperatures at Townsville.

(1934), where size and test thickness distinguished an "inshore race" of *Echinus esculentus*.

Direct comparison of the growth rate of *A. placenta* with the results of growth studies on other echinoids is difficult because of marked species differences in size and shape. In Table 2

the increase in size per annum is expressed as a percentage of the diameter for the preceding year for selected species. The data for *Mellita* are possibly those most relevant, inasmuch as this species is similar in shape to *Arachnoides* in contrast to the spherical form of the other species listed.

TABLE 2

COMPARISON OF GROWTH RATES OF SELECTED ECHINOIDS

	PERCENTAGE INCREASE IN DIAMETER					
YEAR	*Echinus* (Moore, 1935)	*Psammechinus* (Bull, 1938)	*Strongylocentrotus* (Norway) (Greig, 1928*)	*Strongylocentrotus* (Maine) (Swan, 1958)	*Mellita* (Crozier, 1920)	*Arachnoides*
2	36	30	150	176	30	22
3	12	12	60	68	14	19
4	10	3	33	25	43	
5	14	23	25			
6		5	20			

* Quoted by Hyman (1955).
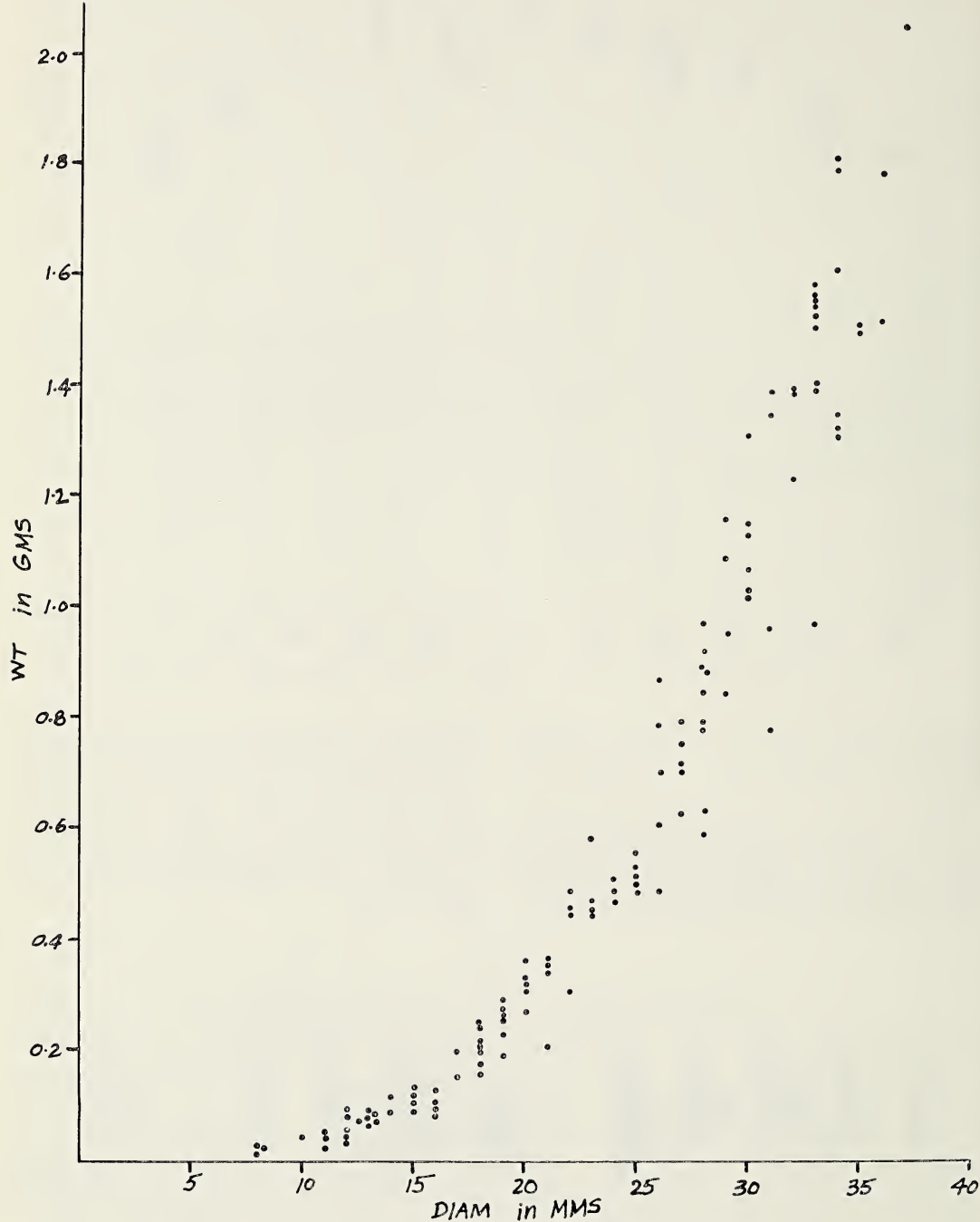
FIG. 4.   Diameter and weight relationship for *A. placenta*.

It would appear that the percentage increase in diameter during the second year is less for *Arachnoides* than for other echinoids. Those species inhabiting cooler waters apparently grow more rapidly than do the tropical *A. placenta,* but by the end of the third year *Mellita,* a warm water echinoid, and *Arachnoides* present a similar picture.

The diameter-to-weight relationship for *A. placenta* approximates the expected cubic form and is similar to that expressed by Swan (1958) for *Strongylocentrotus droebachiensis.* However, the wide range of weight values for any one diameter makes it difficult to reduce the relationship to a series of separate equations as Swan (1958) has done for the Maine species.

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A New Siphonophora, *Vogtia kuruae* n. sp.[1]

ANGELES ALVARIÑO

THE GENUS *Vogtia* Kölliker is represented by four species: *Vogtia pentacantha* Kölliker, 1853; *V. spinosa* Keferstein and Ehlers, 1861; *V. serrata* (Moser), 1925; and *V. glabra* Bigelow, 1918.

The most useful diagnostic feature of the nectophores of the first three species has been described as being angular, prismatic, and pentagonal (Table 1). The last species, *V. glabra*, has rounded nectophores which are rather similar to those of *Hippopodius hippopus*. Bigelow and Sears (1937) described the first three species above as "the three angular belled species." Actually that characteristic is most conspicuous in *Vogtia kuruae* n. sp. Holotype: USNM Catalogue Number 52609; Paratype: USNM Catalogue Number 52610.)
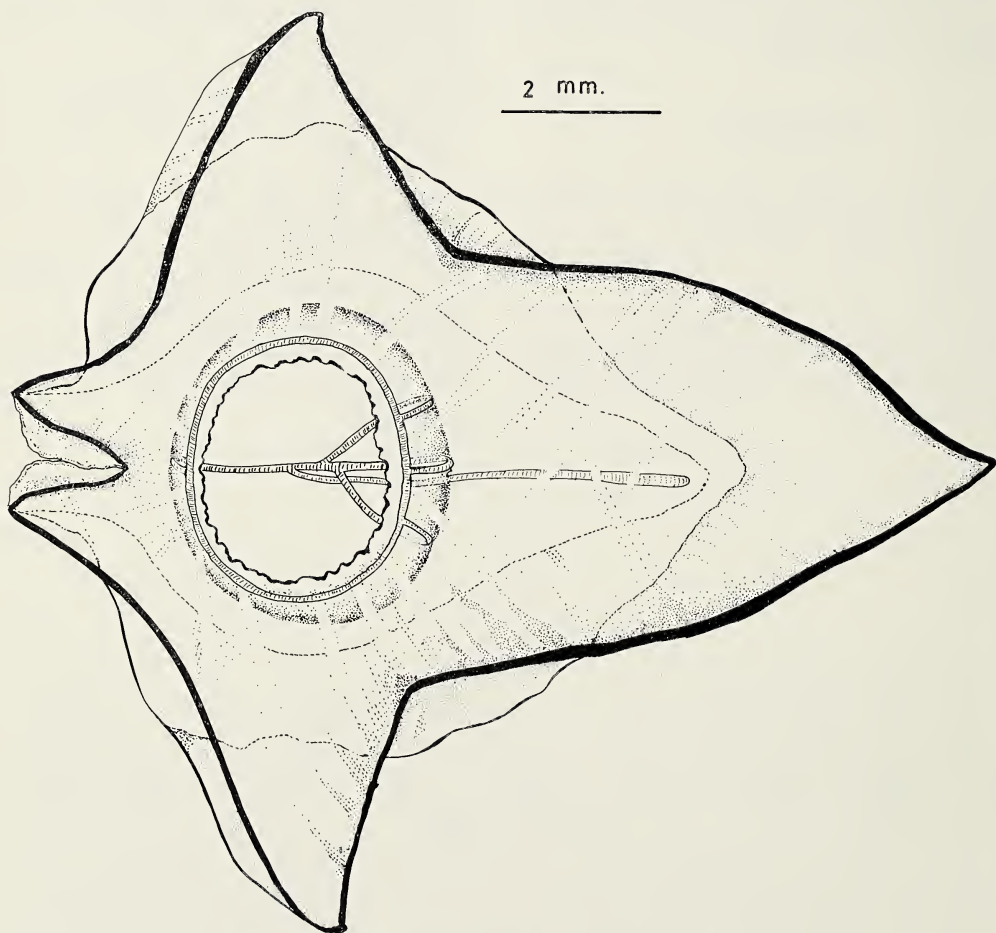
FIG. 1.   Young nectophore of *Vogtia kuruae* n. sp.

TABLE 1

GENERAL CHARACTERISTICS OF THE NECTOPHORES OF FOUR SPECIES OF *Vogtia**

V. pentacantha KÖLLIKER	*V. spinosa* KEFERSTEIN AND EHLERS	*V. serrata* (MOSER)	*V. kuruae* N. SP.
Pentagonal, prismatic, ridges with prominences; facets smooth.	Pentagonal, prismatic; facets and ridges with conical gelatinous prominences.	Angular, prismatic; ridges serrated, facets smooth.	Prismatic, star-shaped; both ridges and facets smooth, without serrations or conical prominences.
Ventral channel joins the dorsal one at about the first 1/4 of the nectosac.	Ventral channel joins to the dorsal channel at about the first 1/8 of the nectosac.	Ventral channel joins the dorsal one at about the first 1/3 of the nectosac.	Ventral channel joins the dorsal one at about the middle of the nectosac.

* *Vogtia glabra* Bigelow is not included in this comparison because it has rounded nectophores.

The nectophores of *V. kuruae* n. sp. present an outline like a three-pointed star. Three isosceles triangles are arranged surrounding the nectosac in such a way that the imaginary bases or smallest side of the triangles circumscribe the nectosac (Figs. 1 and 2). These nectophores thus display the most exaggerated angular shape of all the previously described species, where the three-pointed shape is already incipient. In this species both edges and facets are completely smooth, without protuberances, spines, or serrations.

On the dorsal part of the nectophores appears the nectosac, a shallow cavity outlined as a quite

2 mm.
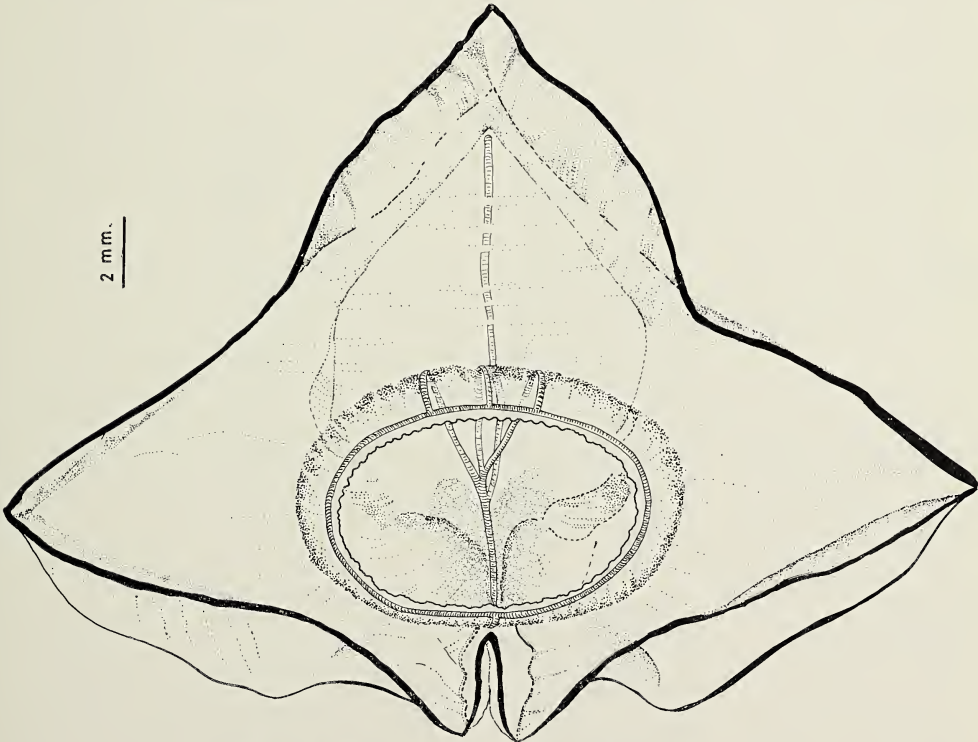
FIG. 2. Adult nectophore of *Vogtia kuruae* n. sp.

TABLE 2

DISTRIBUTION OF *Vogtia kuruae* N. SP.

EXPEDITION OR CRUISE	POSITION	DEPTH IN METERS	STATION
Pacific Ocean			
Downwind	46°35′S, 113°12′W	2010–0	20a
1957	23°39′S, 118°12′W	514–0	37
Monsoon*	49°26′S, 132°18′E	1878–0	13
1960–1961	49°21′S, 132°39′E		
Shellback	9°52.5′S, 81°32′W	313–0	125
1952	12°59′S, 85°01′W	311–0	144
	8°07′S, 84°58′W	176–0	149
	4°05′S, 85°00′W	298–0	153
Tethys	21°33′N, 123°02′W	1500–0	4
1960	21°21′N, 123°12′W		
	18°44′N, 124°24′N	2586–0	5
	18°16′N, 124°24′W		
	7°47′N, 129°37′W	3114–0	9
	7°26′N, 129°34.5′W		
	10°09′N, 147°08′W	868–0	19
	10°35′N, 147°29.6′W		
	26°13.9′N, 141°34.5′W	3000–0	28
	26°22.1′N, 141°06.9′W		
	29°01.2′N, 132°09′W	3000–0	31
	29°11.6′N, 131°41.5′W		
	30°47.6′N, 125°25′W	868–0	33
	30°59′N, 124°53.8′W		
Transpac**	47°35.7′N, 167°44.8′E	510–340	49C
1953	same	680–510	49D
	same	1015–0	
	44°06′N, 161°39′E	653–490	59D
	44°09′N, 152°56.8′E	675–435	66D
Troll***	17°59′N, 134°24′E	200–0	21
1955	15°56′N, 132°27′E	200–0	22
	15°17′N, 124°17′E	200–0	33
	20°43′N, 123°29′E	200–0	35A
	29°54′N, 132°45′E	200–0	41A
	28°28′N, 135°52′E	200–0	43A
CalCOFI	32°50′N, 120°42′W	140–0	87.65
Cruise 5804	31°27′N, 121°57.5′W	420–0	90.90
	29°40′N, 120°52′W	618–0	100.90
Naga	6°23′N, 102°11′E	176–0	60–324
1959–1961	9°54′N, 110°34′E	630–0	60–525
Indian Ocean			
Monsoon	18°49′S, 88°05′E	1643–0	6
1960–1961	18°41′S, 87°51′E		
	33°19′S, 72°34′E	1878–0	9
	33°38′S, 72°31′E		
	36°35′S, 95°28′E	2000–0	11
	36°32′S, 95°52′E		

TABLE 2 (*Continued*)

EXPEDITION OR CRUISE	POSITION	DEPTH IN METERS	STATION
Atlantic Ocean			
Lusiad	00°56′N, 11°29′W	2300–0	79
1963	01°25′N, 11°43′W		
	18°58′S, 10°15′W	2000–0	55
	18°30′S, ———		
	19°13′S, 13°44′W	2000–0	52
	18° 58S′, 13°37′W		
	30°09′S, 04°42′W	3500–0	24
	30°07′S, 05°15′W		
	32°30′S, 09°04′E	3400–0	14
	32°24′S, 08°25′E		
	33°47′S, 15°48′E	2000–0	11
	33°46′S, 15°29′E		

* This species did not appear in the one-meter net oblique tows taken from various depths (356–200 m) to the surface. The records included correspond to mid-water trawls.
** In the small number of stratified samples obtained during this expedition, the species occurred in only a few, and always at depths below 300 m.
*** It is interesting to note that the species occurred in the upper 300 m in the tropical regions, or in zones of upwelling in subtropical waters (CalCOFI records). This emergence of the populations in the tropical regions is not apparently related to either temperature or salinity; but it might be associated with the oxygen concentration, or indirectly with the inorganic-organic phosphate-phosphorus (see Reid, 1965: Figs. 2–5).

perfect circle. In the nectosac the four radial channels follow nearly direct courses, as in *Hippopodius hippopus*. There is a crescent ventral sinus, which appears mostly in an M shape, a distinctive characteristic of the species, but in most of the nectophores it is not clearly seen.

Sometimes the middle pyramid of the nectophores is more enlarged (Fig. 1) than the others (as in Bigelow, 1931: Fig. 190). This might be related to the age of the nectophore.

The five loose nectophores collected at Cocos (4°56′N, 84°35′W), provisionally referred to *V. serrata* Moser by Bigelow (1931), probably belong to the present species, "because they entirely lack the large conical gelatinous spines so characteristic of *V. spinosa* and of *V. pentacantha*" and because of "their peculiarly elongated outline with pyramidal apex, much more prominent than in any *Vogtia* previously described."

Likewise, the nectophores determined as belonging to *V. pentacantha* (Bigelow, 1913) later corrected to *V. serrata* (Bigelow and Sears, 1937) might be *V. kuruae*, especially those shown in Bigelow's Plate 5, Figure 9. Bigelow (1913) stated, "In *pentacantha* the surfaces of the facets are smooth at all ages," and later he added, "But in the present species the older

nectophores have no spines at all. The ridges, like the facets are perfectly smooth, though in the very youngest nectophores the margins of the facets are always ? more or less irregular, and I found one in which they are distinctly spinous." It could be that Bigelow's (1913) material included both *V. pentacantha* or *V. serrata* and the present species, because his Figure 9 in Plate 5 is rather different from the others, and similar to *V. kuruae*. In *V. kuruae* n. sp. I found that both young and old nectophores present smooth ridges and facets, a characteristic which does not correspond to any of the existing described species.

The nectophores of the four species previously described differ in details of form, as is clearly shown when comparing the present figures of *V. kuruae* with the published descriptions of the other species. See Bigelow, 1911: 210, pl. 15, figs. 5–13; 1913:66, pl. 5, figs. 7–8; 1918:405, 406, 407, pl. 4, figs. 1–7; 1931:537, 538; Browne, 1926:61; Chun, 1897:35, pl. 1, figs. 11–14; Haeckel, 1888:177, 182, 364, pl. 29, figs. 9–14; Keferstein and Ehlers, 1861:24, pl. 5, figs. 16–17; Kölliker, 1853:31, pl. 8, figs. 1–8; Leloup, 1933:17, 18, 19; 1934:6; Moser, 1925:420, pl. 27, figs. 6–8, pl. 28, figs. 8–9; Totton, 1932:331.

DISTRIBUTION OF *V. kuruae* N. SP.

Loose or interlocked nectophores of this species have been found in plankton samples collected and analyzed during a number of expeditions as shown in Table 2.

The fact that *V. kuruae* is more abundant in deep tows suggests that it is characteristically a deep water species.

Data on the bathymetric distribution of this species were taken off California (30°30′N, 120°00′W). The stratified samples were collected with the BONGO or BMOC open-closing net (McGowan and Brown, 1966) at various depths during August 27 and 30, and September 1, 2, 3, and 5, 1965. During these series of collections, *V. kuruae* did not occur in samples collected in the upper 300 m, nor in the samples from below 1030 m. It did occur in samples taken at 460–410, 500–420, 620–530, 775–685, and 1030–860 m.

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The Systematics of the Prickly Sculpin, *Cottus asper* Richardson, a Polytypic Species
Part I. Synonymy, Nomenclatural History, and Distribution[1]

Richard J. Krejsa[2]

ABSTRACT: The prickly sculpin, *Cottus asper,* is a geographically widespread, polytypic species characteristically represented by very prickly, nonmigratory, freshwater spawning "inland" forms, and less prickly, catadromous, brackish-water spawning "coastal" forms. Part I, the first contribution in a series on the systematics of this species, presents a synonymy complete for the period 1836–1936, with a resumé of the most important citations from 1936 to 1965. A nomenclatural history of the species is given. The distributional range is listed and also presented in illustration.

THE PRICKLY SCULPIN ranges over about 3,000 miles of Pacific North Temperate coastline and inland as far as 300 miles. The species exists in two primary modes of morphological variability: one, a nonmigratory, fresh-water spawner, has extensive squamation on certain regions of the body; the other, a catadromous, brackish-water spawner, has little or none. Prickly sculpin eggs are spawned naturally in environments which are known to vary in at least one major factor, i.e., salinity. The morphological, behavioral, and ecological variations existing within this species make it an excellent subject for systematic analysis.

SYNONYMY

It has been 130 years since *Cottus asper* was first described by Sir John Richardson. Prior to the present study, regional systematic treatments of this widespread species resulted in a proliferation of generic and specific taxa, all referable to *C. asper.* Early revisionary work by Girard in 1851 and 1852 was incomplete because of lack of specimens. Recent regional works (Robins and Miller, 1957; McAllister, 1957; McAllister and Lindsey, 1959; and Bond, 1963) have included the species as part of a geographical area or river drainage system, but there has never been a comprehensive treatment of the species throughout its entire range. In the period 1836–1936, 41 reports of *C. asper* were cited in the literature. In the same period, 32 additional citations occurred which were either misidentifications or synonyms properly referable to *C. asper.* In none of the systematic treatments published since the original description in 1836 has there been a synonymy containing more than 7 citations. McAllister (1957) listed 15 citations in his unpublished M.A. thesis.

The present synonymy consists of 73 citations published during the period 1836–1936, and is thought to be complete for that period. In the past 30 years, the species has been cited incidentally in so many fishery journals and publications that only the major systematic, or otherwise noteworthy, citations have been reported in the remaining synonymy.

Cottus asper Richardson, 1836

Cottus asper. Richardson, 1836:295, pl. 95, fig. 1 (original description and figure; Columbia R.; collected by Dr. Gairdner, probably near Fort Vancouver, Washington Territory). Storer, 1846a:260, and 1846b:8 (northwestern coast of N. America). Girard, 1850:409, and 1851a:189 (discusses propriety of present

nomenclature). Eigenmann, 1895:118 (abundant in Fraser system from tidewater to 1,900 ft; Mission, Sicamous, Kamloops, and Griffin L., British Columbia; and Umatilla, Oregon). Gilbert and Evermann, 1895:201 (description; comparison with Sacramento R. form; Walla Walla R. at Wallula, and Lake Washington, Washington). Seale, 1896:854 (Lake Washington). Gilbert, 1896:418 (description; stream entering Departure Bay, Vancouver Island). Jordan and Evermann, 1896: 439 (synonymy; streams of the Cascade Range, from Vancouver Island to Oregon). Gilbert, 1898:1 (Columbia R.; notes absence in Klamath R.). Jordan and Evermann, 1898:1944 (description; synonymy; Walla Walla; Departure Bay; about Port Townsend; streams of the Cascade Range, from Vancouver Island to Oregon). Evermann and Meek, 1898:83 (Lake Washington). Meek, 1899:231 (Lake Southerland, Olympic Peninsula, Washington). Jordan, 1905:445 (streams of the Pacific coast). Snyder, 1905:337 (description; affinities; habitat preference; San Franciscito, Madera, San Antonio, Guadalupe, Coyote, and Alameda creeks, all flowing into San Francisco Bay). Evermann and Goldsborough, 1907a:306 (characters; prickling descriptions; Deep Bay, Naha R., and Steelhead Cr., Loring, Alaska; Hunter Bay, Yes Bay, and McDonald L., Alaska). Evermann and Goldsborough, 1907b: 110 (Fraser R. at Mission, Shuswap L. at Sicamous, Thompson R. at Kamloops, and Griffin L.). Rutter, 1908:145 (Cottopsis parvus first placed in synonymy with asper; synonymy, in part, except Uranidea semiscaber (sic) centropleura Eigenmann and Eigenmann; summary of 9 localities in Sacramento R. system). Snyder, 1908a:269 (Russian R., California). Snyder, 1908b:184 (characters; prickling description; summary of 41 localities: from Lake Washington, Columbia and Sacramento R., and river basins in between). Nichols, 1909:172 (head of Chilkoot L., Alaska). Evermann and Latimer, 1910:138 (4 localities in Marin Co., and 2 localities in San Francisco Bay, California; 12 localities in Olympic Peninsula, Washington). Snyder, 1913:72 (characters; Pajaro R., California). Snyder, 1916:381 (Papermill and Walker creeks, California). Kermode, 1917:20 (Hanceville, British Columbia [Chilcotin R.

drainage]). Jordan, 1919:249 (designates Cottus asper Richardson as the orthotype of Cottopsis Girard). Bean and Weed, 1920:76 (mouth of Fraser R.). Hubbs, 1921:7 (re-identification of San Luis Cr., California, specimens misidentified by Jordan as C. gulosus [1895:141]; range extension to Ventura R., California). Fowler, 1923:282 (Hanceville, and Shawnigan L., British Columbia; Shawnigan L. specimen misidentified by Kermode [1909:87] as Uranidea gulosa). Crawford, 1927:177 (streams flowing into Puget Sound). Schultz, 1929:48 (listing only). Schultz, 1930: 14 (most streams and lakes of western Washington). Jordan, Evermann, and Clark, 1930: 383 (synonymy; streams of the Cascade Range, southeastern Alaska to Oregon; south to Sacramento R.). Kermode, 1931:19 (Cowichan L., Vancouver Island). Evermann and Clark, 1931: 56 (summary of 32 recorded localities in California). Taft, 1934:251 (spawning migration). Schultz and DeLacy, 1936a:128 (synonymy; coastal streams from Alaska to Ventura Co., California; fresh water and brackish water; review of most records from Puget Sound to Oregon, and addition of 26 more localities). Schultz and DeLacy, 1936b:213 (additional synonymy; 3 new localities). Schultz, 1936:179 (keys to species of Cottus; coastal streams from Alaska to Ventura Co., California; fresh-water and brackish). Dymond, 1936:71 (description; throughout southwestern British Columbia, including southern Vancouver Island; 16 localities listed). Sumner, 1942:1–25 (common in tidewater areas along the Oregon coast). Hubbs and Wallis, 1948:141 (identification of "Cottus sp." recorded by Dill, 1946:54). Bailey and Dimick, 1949:14 (comparison with Cottus hubbsi). Shapovalov and Dill, 1950:387 (listing only). Wilimovsky, 1954:285 (southeast Alaska to California). Robeck, et al., 1954: B–65 (Columbia R., above Trinidad, Washington; cited as "prickly sculpins Cottus sp.," these may include Cottus rhotheus in part). Lindsey, 1956:777 (Pacific Slope of N. America from Alaska to California; British Columbia mainland from Columbia, Fraser, and Skeena systems, Stikine R. headwaters, and Peace R. [Summit L., Heart L., Angusmac Cr., and McLeod L.]). Robins and Miller, 1957:229 (Cottopsis parvus again removed from syn-

onymy of *C. gulosus*). Lindsey, 1957:657 (British Columbia: Columbia R.; Fraser R.; Skeena R.; coast drainages south of Skeena; Nass R.; Stikine R.; Peace R.). Wilimovsky, 1958:62 (key to species in Alaska; southeast Alaska to California). Shapovalov, Dill, and Cordone, 1959:173 (listing only). Carl, Clemens, and Lindsey, 1959:158 (description; Pacific drainages from Chilkoot L., Alaska, to Ventura R., California. In British Columbia: lakes and rivers of the Columbia, Fraser, Dean, Skeena, Nass, and Stikine systems; coastal rivers of the mainland and Vancouver Island, and Queen Charlotte Islands; headwaters of Peace R. system from Summit L. to McLeod L.). McAllister and Lindsey, 1959:70 (description; synonymy; intraspecific variation; localities as in Carl, Clemens, and Lindsey, 1959). McAllister, 1960:42 (collection in salt water, Pt. Atkinson, British Columbia). Bond, 1961:36 (key to species in Oregon; prickling variation; Columbia R. drainage). Bond, 1963: 79 (synonymy; life history observations; oxygen, temperature, and salinity tolerance of adults; fish associates; habitat preference; lists 35 new collection localities in coastal Oregon, 30 localities from Columbia R. drainage in Oregon, and also some lakes in the southwest corner of Rainier National Park, Washington). Bailey and Bond, 1963:19 (recognition of several species groups within *Cottus* in western N. America; characters and list of species in the "*asper* species group"). Krejsa, 1965:1–109 (synonymy; nomenclatural history; distribution; life history; morphological variation; salinity tolerance of eggs; phylogeny of *C. asper* and closely related species). Bohn and Hoar, 1965: 977 (salinity effects on iodine metabolism; physiological divergence of inland and coastal *C. asper*).

Centridermichthys asper. Richardson, 1844:76 (River Oregon [= Columbia R.]). Günther, 1860:170 (description; synonymy; fresh waters of the Oregon and Washington Territories). Lord 1866*a*:130 (life history; spawning behavior, in part; Puget Sound; "streams flowing through the Sumass and Chilukweyuk prairies" [Sumas and Chilliwack R. ?], British Columbia; in part, all streams east and west of the Cascades).

Cottopsis asper. Girard, 1851*b*:303 (introduction of *Cottopsis* gen. nov.; synonymy; limited to River Oregon [= Columbia R.]). Girard, 1851*c*:185 (not seen). Girard, 1852:61 (definition of *Cottopsis* gen. nov., based on Richardson's description of *Cottus asper*; synonymy; Columbia R.). Girard, 1859:51 (description; synonymy; based on 8 specimens from Astoria and Fort Dalles, Oregon, and Fort Steilacoom, Puget Sound, Washington Territory). Suckley (in Cooper and Suckley, 1859) 1859:351, and Suckley, 1860:351 (description; synonymy; small fresh-water streams emptying into Puget Sound; Ft. Steilacoom; and Columbia R., 200 miles above mouth). Jordan and Jouy, 1882:5 (Puget Sound; Columbia R.; Mare Island and Sacramento R., California).

Uranidea aspera. Jordan and Gilbert, 1883:694 (description; synonymy; streams west of the Sierra Nevada and Cascade Mountains). Jordan, 1885: 110 (subgenus *Cottopsis* and a list of species therein).

Trachidermus richardsonii. Heckel, 1840:162 (synonymy; Columbia R.), (not *Cottus richardsoni* of Agassiz, 1850). Note: Girard, 1852:62, erred in reporting the date of Heckel's paper as 1837, and in the spelling of *Trachidermus*.

Cottopsis parvus. Girard, 1856*b*:144 (original description; Presidio on San Francisco Bay, California). Girard, 1857:11 (description; Presidio, and Monterery, California). Girard, 1859:54 (description; synonymy; Monterey, Presidio, Fort Reading, and Petaluma, California). Cooper, 1868:492 (listing only). Jordan, 1877:5 (as the young of *Cottopsis asper*).

Centridermichthys parvus. Günther, 1860: 170 (description; synonymy; fresh waters of California). Lord, 1866*b*:352 (listing; "frequenting the same localities as . . ." *Centridermichthys asper*).

Uranidea aspera var. *parvus*. Jordan and Gilbert, 1883:694 (Sacramento R. forms).

Cottus gulosus parvus. Jordan and Evermann, 1898:1945, and Jordan, Evermann, and Clark, 1930:383 (*Cottopsis parvus*: Monterey, Presidio, Fort Reading, and Petaluma, California).

Uranidea gulosa, in part. Jordan and Gilbert, 1883:695 (misidentifications: all specimens from "Vancouver's Island" and probably those from "about Port Townsend," cf. Jordan and Evermann, 1898:1944). Kermode, 1909:87 (listing only; misidentification: Shawnigan L., Vancouver Island, cf. Fowler, 1923:282).

Cottus gulosus, in part. Jordan, 1895:141 (misidentification: San Luis Cr., near Avila, California, cf. Hubbs, 1921:7). Jordan and Evermann, 1898:1945 (misidentification: all specimens from San Franciscito Cr., Santa Clara Co., California). Jordan, Evermann, and Clark, 1930:383 (probable misidentifications: specimens from Loring and Boca de Quadra, Alaska). Evermann and Clark, 1931:57 (misidentifications: Presidio, Monterey, Fort Reading, Petaluma, and San Luis Cr., California). Evermann and Clark, 1931:12, 13 (misidentifications: Monterey, Presidio, Fort Reading, and Petaluma). Bean and Weed, 1920:76 (questionable identification: 4 specimens from Victoria, Vancouver Island, British Columbia). Wilimovsky, 1954:285 (doubts validity of southeast Alaska record).

Centridermichthys gulosus. Lord, 1866*b*: 352 (listing; "frequenting the same localities as . . ." *Centridermichthys asper*).

Cottus sp. Dill, 1946:54 (San Joaquin R., near Friant, California; identification as *asper* by Hubbs and Wallis, 1948:141).

NOMENCLATURAL HISTORY

The specific name *asper* is currently well founded in the genus *Cottus,* to which it was originally designated by Richardson in 1836. But, as shown in the preceding synonymy, the binomen was extremely unstable for the first 100 years after its introduction. After an initial period of uncertainty regarding its affinity to marine or to fresh-water Cottoids, three main nomenclatural difficulties are encountered: the often-repeated misidentification as *Cottus gulosus* (Girard); the failure to recognize that *Cottopsis parvus* and *Cottus asper* are conspecific; and the failure to recognize the specific relationship of *asper* to other species in the genus *Cottus.*

The almost immediate placement of *asper* into *Trachidermus* by Heckel (1840), and then into the synonymous *Centridermichthys* by Richardson (1844), reflects the early opinion that *asper* was more closely allied to the marine Cottoids. Girard (1851*b*, 1852) recognized its affinities with the fresh-water genus *Cottus,* but distinguished it from that genus by erecting the genus *Cottopsis,* based on the presence of palatine teeth and the "skin beset with prickles, instead of being smooth and scaleless." Lacking any specimens, Girard defined *Cottopsis* on the basis of Richardson's original description but, on p. 63, where he quoted Richardson's entire discussion of prickles (p. 295), he misquoted Richardson by attributing to him the statement, "There are no scales." Girard's lack of specimens proved unfortunate since soon thereafter (1856*b*) he named and described *Cottopsis parvus* from the Presidio (in San Francisco), California, comparing it not with *C. asper* but with *Cottopsis gulosus* Girard, also newly described (1856*a*) from the San Joaquin R., California. In his later report (1859), Girard had 8 specimens of *C. asper* in his possession, from the Columbia R. and Puget Sound. Obviously he again failed to recognize the conspecificity of *asper* and *parvus,* and he followed Richardson's original description rather than comparing them with specimens of *parvus,* which he seems to have reserved for comparison with *gulosus.*

Jordan (1877) referred, in passing, to *Cottopsis parvus* as the young of *C. asper.* Jordan and Jouy (1882), however, listed specimens of *Cottopsis asper* from Mare Island and Sacramento R., California, *and* from Puget Sound and the Columbia R. Less than a year later, Jordan and Gilbert (1883) placed *asper* in the genus *Uranidea* DeKay, subgenus *Cottopsis,* based on the presence of palatine teeth and the gill membranes being broadly united to the isthmus. In the same report, they referred to the Sacramento R. form of *U. aspera* as "var. *parvus,* smaller in size, paler in color and with the interorbital space concave, narrower than eye."

Eigenmann (1895) used the valid name to describe specimens from the Fraser and Columbia rivers, as also did Gilbert and Evermann (1895), who suggested that the nominal spe-

cies was separable "at least subspecifically from the Sacramento River form." Seale (1896) and Gilbert (1896) used the valid name for northern specimens. But, obviously, Jordan (1895) and Jordan and Evermann (1896) still thought in terms of a distinct Californian species (*gulosus*) and a distinct northern species (*asper*). Jordan misidentified a specimen of *asper* from San Luis Cr., near Avila, Calfornia, as *gulosus*. Jordan and Evermann listed the range of the nominal species from Vancouver Island to Oregon, and of *gulosus,* from California Coast Range streams and inland in the San Joaquin R. Gilbert (1896) referred to *Cottus asper* of the Columbia and *Cottus gulosus* of the Sacramento as "two species so extremely similar that it is difficult to distinguish them." Jordan and Evermann (1898) repeated the suggestion of Gilbert and Evermann that the nominal species is separable, at least subspecifically, from the Sacramento R. form, "*Cottus gulosus*."

That Jordan and Evermann perceived neither the conspecific relationship of *parvus* to *asper* nor the limits of the valid species *Cottus gulosus* becomes more fully evident on the next page (p. 1945) of their 1898 report. Their description of *Cottus gulosus* (Girard) is taken from misidentified specimens of *C. asper* collected in San Franciscito Cr., Santa Clara Co., California. These were large specimens "3 to 7 inches in length" and, most significantly, the count for anal rays is given as "A. 16 to 18." Both of these characters separate *asper* from *gulosus*. Furthermore, they include *Cottopsis parvus* Girard, from Monterey, the Presidio, Fort Reading, and Petaluma, California, in the synonymy of *gulosus*.

Snyder (1905) collected and correctly identified *Cottus asper* from the same locality, San Franciscito Cr. He was probably the only one of his time to understand and explain the true relationships of *asper, parvus,* and *gulosus*. On p. 337, he stated:

Recent authors have identified the common Sacramento form which represents the *Cottus asper* of the Columbia River with the *Cottopsis gulosus* of Girard. They have sometimes considered the Sacramento form as identical with *C. asper* and have placed the name *gulosus* in the synonymy of the latter. At other times they have considered the species as a slightly differentiated form worthy of recognition in nomenclature, and have used the name *gulosus* to designate it. The

former view concerning the species is probably correct. The association of the name *gulosus* with it, however, is without warrant. The latter belongs to a species easily distinguished from *C. asper,* differing notably in having a much shorter anal fin. There are usually fewer dorsal spines and rays, a more limited distribution of prickles, and an almost uniform absence of palatine teeth. In *C. asper* the dorsal has 8 to 10 spines and 19 to 22 articulated rays, the anal 16 to 18 rays, while in *C. gulosus* the dorsal has 7 to 9 spines, 17 to 18 rays, the anal 12 to 14 rays.

Snyder then continues with a note on habitat preference:

In its distribution *C. asper* appears to be largely confined to the lower courses of the streams, being especially abundant near tide water, while *C. gulosus* is found further up, where the water is clear and the current rapid.

Rutter (1908) correctly placed *Cottopsis parvus* into the synonymy of *Cottus asper,* presumably recognizing that the two were conspecific. However, he incorrectly synonymized *Uranidea semiscabra centropleura* Eigenmann and Eigenmann, which is properly referable to *Cottus gulosus*.

Snyder was the first to consider a series of specimens of the nominal species throughout its entire range, as then known, and, in the same issue of the Bulletin of the Bureau of Fisheries in which Rutter had correctly synonymized *parvus,* he noted the extreme variation of prickling investment. While recognizing the variation between streams, he also noted that the prickling variation is common among individuals from the same stream.

Although explicitly aware of Snyder's comments on *asper* and *gulosus,* Evermann and Goldsborough (1907a) identified 16 specimens of *gulosus* from Loring and Boca de Quadra, Alaska. The reliability of these identifications is questionable. Kermode's listing (1909) of *Uranidea gulosa* from Shawnigan L., Vancouver Island is probably a misidentification, since Fowler (1923:282) listed the same specimen as *Cottus asper*.

Snyder (1913, 1916) again recorded the occurrence of *C. asper* and *gulosus* in differing habitats of the same stream. Hubbs (1921) recognized Jordan's earlier misidentification of *gulosus* from San Luis Cr., California. He also commented on the variability of prickling in *C. asper* from several streams.

It would seem that with the accession of Snyder's insight into the problem, the valid name was destined for stability. However, Jordan, Evermann, and Clark (1930) repeated the earlier error of Jordan and Evermann (1898) by including *Cottopsis parvus* as a synonym of *Cottus gulosus*. In a similar manner, they also incorporated the error of Evermann and Goldsborough (1907*a*), previously cited, by including the misidentified specimens of *asper* from Loring and Boca de Quadra, Alaska, in the list of records for *gulosus*. In the same work, Jordan and Evermann extended the range of *asper* (cited in 1898 as: "streams of the Cascade Range, from Vancouver Island to Oregon") by appending the phrase "south to Sacramento River." Evermann and Clark (1931) also retained *Cottopsis parvus* in the synonymy of *C. gulosus* and perpetuated Jordan's misidentification of the San Luis Cr. *gulosus,* which Hubbs had correctly re-identified as *asper* ten years before (1921).

Schultz and DeLacy's catalogue (1936) included a comprehensive listing of Washington and Oregon localities for *C. asper.* However, some remain doubtful since Schultz and DeLacy frequently misidentified *C. asper* as *gulosus* and/or *perplexus.* They also incorrectly maintained the presence of *C. gulosus* in Alaska.

Robins and Miller (1957) presumably overlooked the earlier citation of Rutter (1908) and removed *Cottopsis parvus* from the synonymy of *gulosus,* placing it in the synonymy of *asper,* supposedly for the first time.

McAllister and Lindsey (1959) first suggested the probable existence of "coastal" and "non-coastal" populations of *Cottus asper* on the basis of morphological and, perhaps, behavioral differences.

Bond (1961) hinted at the possibility of polytypy in *Cottus asper* when he stated in his key that the body is "well covered with prickles, especially in inland waters and in young individuals from coastal waters." Bond (1963) gave the most comprehensive treatment yet recorded for *Cottus asper* and 12 other species in the genus. His study, however, was more concerned with interspecific rather than intraspecific relationships within the genus. Bailey and Bond (1963) indicated their concern for the supraspecific relationships within the genus

Cottus by their recognition of several species groups, one of which is the "*asper* species group."

Krejsa (1965) offered morphological, behavioral, and distributional evidence for genetic divergence between "coastal" and "inland" populations of *C. asper.* Bohn and Hoar (1965) offered physiological evidence in support of Krejsa's hypothesis. Unfortunately, their brief introductory remarks regarding the life histories and prickling patterns are somewhat inaccurate, and therefore misleading, interpretations of Krejsa's unpublished thesis. These minor points will be clarified in a future publication.

DISTRIBUTION

Range. Pacific Slope drainage of North America: coastal streams from Seward, Alaska, to Ventura R., California; lakes and streams of the Queen Charlotte Islands and Vancouver Island; and all major Pacific drainages from the headwaters of the Stikine R. in British Columbia, to the Kern R., San Joaquin R. drainage, California. The following are exceptions: Fraser R. in the area of the Rocky Mountain Trench, east of Prince George, British Columbia (area not yet collected); Kootenay Lake drainage of the Columbia R. in British Columbia; Upper Snake R. of the Columbia R. drainage in Washington and Oregon; Middle Fork of the Willamette R. in Oregon, above Oakridge; Klamath R. Basin in Oregon; and Sacramento R. drainages above Lake Shasta, California. Arctic Slope drainage of North America: headwaters of the Peace R. in British Columbia: from Summit L. to McLeod L., Crooked R. drainage; from Tacheeda L., Parsnip R. drainage; from Tchentlo L., Nation R. drainage.

The present distributional range of *Cottus asper* is illustrated in Figure 1.

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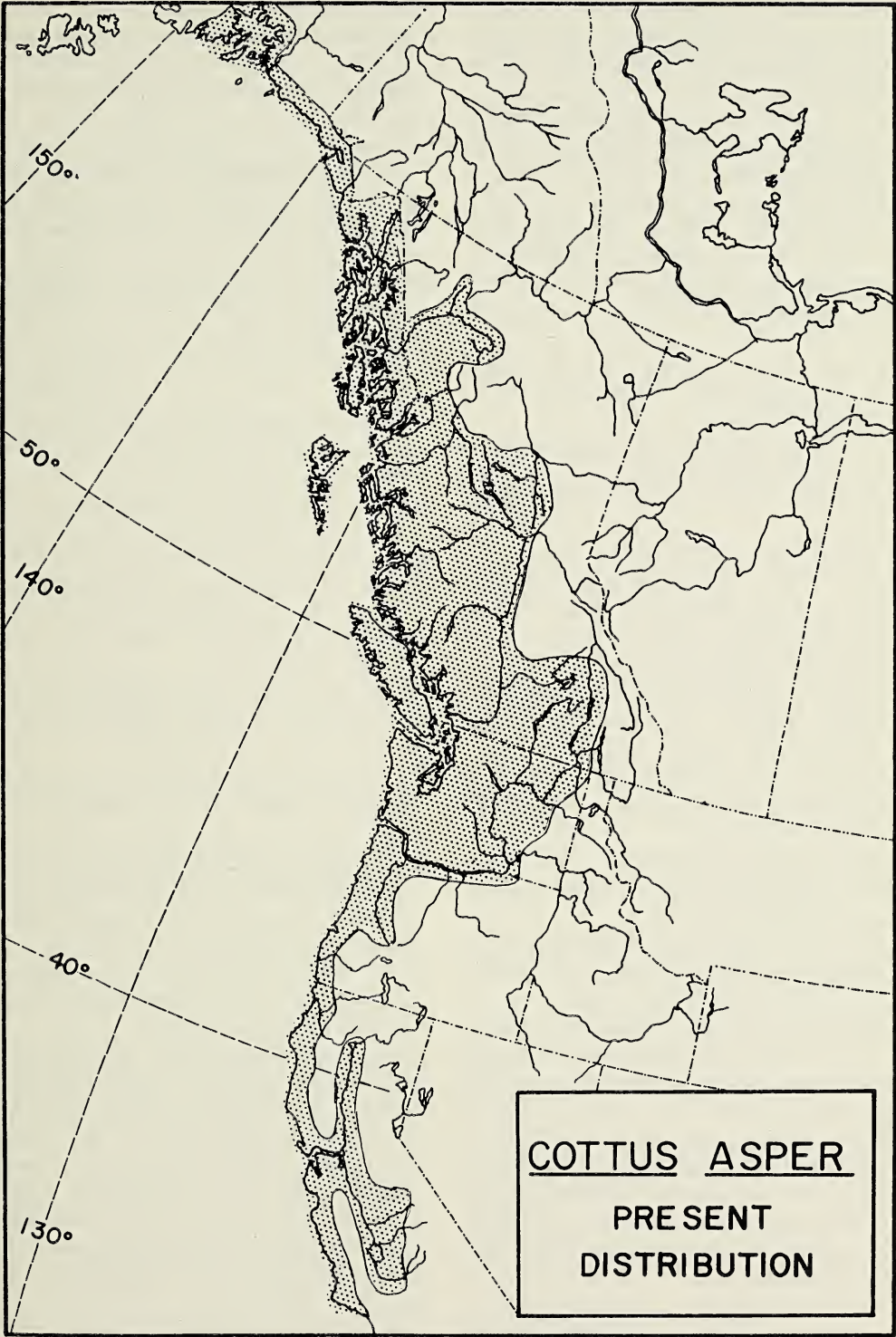
FIG. 1.   Distributional range of *Cottus asper*.

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Chromosomes of Some Opisthobranchiate Mollusks from Eniwetok Atoll, Western Pacific[1]

J. B. Burch[2] and R. Natarajan[3]

ABSTRACT: Chromosome numbers are reported for nine species of opistho-branchiate mollusks from Eniwetok Atoll, Marshall Islands, western Pacific. In the Nudibranchia, both *Dendrodoris nigra* (Dendrodorididae) and *Herviella mietta* (Favorinidae) were found to have 13 bivalents during male meiosis. In the Anaspidea, *Dolabrifera dolabrifera* and *Stylocheilus longicauda* (Aplysiidae) both had 17 bivalents during male meiosis. In the Cephalaspidea, *Haminoea linda* and *H. musetta* (Atyidae) each had 17 pairs of chromosomes during male meiosis and *Lathophthalmus smaragdinus* and *Smaragdinella calyculata* (Smaragdinellidae) had 18 pairs. In the Soleolifera, *Onchidella evelinae* had 18 bivalents during male meiosis.

The extreme conservativeness of chromosome numbers in opisthobranchiate mollusks is demonstrated by that fact that all 18 nudibranchs from 10 families studied so far have the single haploid chromosome number 13, and that 18 of the 21 species of the orders Entomotaeniata, Anaspidea, Cephalaspidea, and Sacoglossa have 17 pairs of chromosomes. The haploid number 18 is here reported for the first time for nonsoleoliferan opisthobranchiate mollusks. The more advanced, mostly fresh-water, order Basommatophora, in which the haploid number 18 is the basic number, may well have been derived from a taxon within or related to this cephalaspid superfamily (Philinacea).

IN RECENT YEARS, detailed investigations have been made on the chromosomes of many basommatophoran and stylommatophoran snails (Burch, 1965), but relatively few species of the opisthobranchiate[4] orders have been studied,

mainly because of the difficulties they present in collection and identification. Relying on the studies of various authors during the early part of the present century, Makino (1951) listed the chromosome numbers of 16 opisthobranchiate species, but recent investigations by Inaba and our present studies indicate that the earlier records are not dependable and so are obsolete. Previous reliable reports on the chromosomes of opisthobranchiate gastropods are those of Inaba and Hirota (1954, 1958), Inaba (1959a, 1959b, 1961), Natarajan (1959, 1960), Mancino and Sordi (1964a and b), and Burch (1965). These authors give the chromosome numbers of 36 species belonging to 21 families and 7 orders (Tables 1 and 2). This is a very small number when compared with the great multitude of species currently recognized in the opisthobranchiate orders. The present paper presents the chromosome numbers of 9 opisthobranchiate

[4] Boettger (1955) considers the orders Opistho-branchiata and Pulmonata (together equivalent to the subclass Euthyneura) to be unnatural ones, and instead divides the Euthyneura into seven orders. While we do not disagree with this, it is still convenient to speak of his five lower (mainly marine) euthyneuran orders (Nudibranchia, Soleolifera, Cephalaspidea, Sacoglossa, and Anaspidea) as "opistho-

branchs" as distinguished from the more advanced Basommatophora (mainly freshwater) and Stylommatophora (land inhabitants).

TABLE 1

CHROMOSOME NUMBERS PREVIOUSLY REPORTED IN THE OPISTHOBRANCHIATE ORDERS
NOTASPIDEA AND NUDIBRANCHIA

SPECIES	CHROMOSOME NUMBER		LOCALITY	REFERENCE
	2n	n		
NOTASPIDEA				
Pleurobranchidae				
Pleurobranchaea				
novaezealandiae	24	12	Japan	Inaba, 1959*a*
NUDIBRANCHIA				
Dorididae				
Glossodoris festiva		13	Japan	Inaba and Hirota, 1958
Glossodoris pallescens		13	Japan	Inaba and Hirota, 1954; 1958
Rostanga arbutus	26	13	Japan	Inaba, 1959*a*
Discodoris pardalis		13	Japan	Inaba, 1959*a*
Doris verrucosa	26	13	Italy	Mancino and Sordi, 1964*a*
Dendrodorididae				
Dendrodoris miniata	26	13	Japan	Inaba and Hirota, 1958
Dendrodoris nigra	26	13	Japan	Inaba and Hirota, 1958; Inaba, 1959*b*
Triophidae				
Kaloplocamus ramosus		13	Japan	Inaba and Hirota, 1958
Plocamopherus tilesii	26	13	Japan	Inaba and Hirota, 1958
Goniodorididae				
Okenia barnardi		13	Japan	Inaba and Hirota, 1958
Fimbriidae				
Melibe papillosa	26	13	Japan	Inaba, 1959*a*
Dotonidae				
Doto bella		13	Japan	Inaba, 1961
Arminidae				
Dermatobranchus striatus	26	13	Japan	Inaba and Hirota, 1958
Cuthonidae				
Catriona pupillae		13	Japan	Inaba, 1961
Facelinidae				
Facelina ceylonica		13	Japan	Inaba and Hirota, 1958
Facelina japonica		13	Japan	Inaba and Hirota, 1958

species belonging to 6 families and 4 orders (Table 3), which were collected in shallow waters around three islands of Eniwetok Atoll in the western Pacific by the senior author and Dr. William H. Heard during early 1960.

MATERIAL AND METHODS

The species studied in this investigation and the localities where they were collected are listed below. Duplicate specimens have been deposited in the collections of the Museum of Zoology at the University of Michigan, the University of São Paulo, and the University of Hawaii.

NUDIBRANCHIA

1. *Dendrodoris nigra* (Stimpson) (Fig. 1). North end of Japtan Island, under loose pieces of dead coral. April 1, 1960.

2. *Herviella mietta* Marcus and Burch (Fig. 2). North end of Eniwetok Island on the lagoon side, in about 10 cm of water at low tide, under submerged pieces of dead coral. April 2, 1960.

ANASPIDEA

3. *Dolabrifera dolabrifera* (Rang) (Fig. 3). Under loose pieces of coral on seaward tide flat at the north end of Parry Island. March 25, 1960.

TABLE 2

CHROMOSOME NUMBERS PREVIOUSLY REPORTED IN THE OPISTHOBRANCHIATE ORDERS
ENTOMOTAENIATA, CEPHALASPIDEA, ANASPIDEA, SACOGLOSSA, AND SOLEOLIFERA

SPECIES	CHROMOSOME NUMBER		LOCALITY	REFERENCE
	2n	n		
ENTOMOTAENIATA				
Pyramidellidae				
Tiberia fasciata		17	Japan	Inaba, pers. comm.
ANASPIDEA				
Aplysiidae				
Petalifera punctulata	34	17	Japan	Inaba, 1959a
Notarchus leachii freeri		17	Japan	Inaba, 1959a
CEPHALASPIDEA				
Acteonidae				
Cylichnatys angusta		17	Japan	Inaba, pers. comm.
Philinidae				
Philine japonica		17	Japan	Inaba, 1959a
Aglajidae				
Aglaja gigliolii	34	17	Japan	Inaba, 1959a
SACOGLOSSA				
Elysiidae				
Elysia amakusana		17	Japan	Inaba, 1959a
Elysia viridis		17	Italy	Mancino and Sordi, 1964b
Stiligeridae				
Alderia nigra		17	Japan	Inaba, 1961
Hermaeopsis variopicta		17	Italy	Mancino and Sordi, 1964b
Placida dendritica	34	17	Italy	Mancino and Sordi, 1964b
Placida viridis	34	17	Italy	Mancino and Sordi, 1964b
Stiliger vesiculosus	34	17	Italy	Mancino and Sordi, 1964b
Juliidae				
Berthelinia limax		17	Japan	Inaba, 1961
Polybranchiidae				
Bosellia mimetica	14	7	Italy	Mancino and Sordi, 1964b
SOLEOLIFERA				
Veronicellidae				
Veronicella floridana		16	U.S.A.	Burch, 1965
Laevicaulis alte		17	India	Natarajan, 1960
Onchidiidae				
Oncidiella kurodai		17	Japan	Inaba, 1961
Onchidium verraculatum	36	18	India	Natarajan, 1959

4. *Stylocheilus longicauda* (Quoy and Gaimard) (Fig. 4). In tide flats of Eniwetok Island. March 4, 1960.

CEPHALASPIDEA

5. *Haminoea linda* Marcus and Burch (Fig. 5). Parry Island, in sand, in about 2 m of water, in lagoon, about 17 m from shore. March 31, 1960.

6. *Haminoea musetta* Marcus and Burch (Fig. 6). Middle part of Parry Island on seaward tide flats. April 2, 1960.

7. *Lathophthalmus smaragdinus* (Rüppel and Leuckart) (Fig. 7). Collected at the south end of Parry Island, under loose pieces of coral on seaward tide flat. March 15, 1960.

8. *Smaragdinella calyculata* (Broderip and

SPECIES	CHROMOSOME NUMBER (n)	NUMBER OF SPECIMENS GIVING RESULTS
NUDIBRANCHIA		
Dendrodorididae		
Dendrodoris nigra	13	5
Favorinidae		
Herviella mietta	13 (2n = 26)	1
ANASPIDEA		
Aplysiidae		
Dolabrifera dolabrifera	17	9
Stylocheilus longicauda	17	2
CEPHALASPIDEA		
Atyidae		
Haminoea linda	17	1
Haminoea musetta	17	2
Smaragdinellidae		
Lathophthalmus smaragdinus	18	2
Smaragdinella calyculata	18	2
SOLEOLIFERA		
Onchidiidae		
Onchidella evelinae	18	2

Sowerby) (Fig. 8). In lagoon at north end of Eniwetok Island.

SOLEOLIFERA

9. *Onchidella evelinae* Marcus and Burch (Fig. 9). In cracks in coral slabs above water line (at low tide) on the lagoon side at the north end of Eniwetok Island. April 5, 1960.

The materials examined consisted of ovotestes fixed in either Newcomer's (1953) or Carnoy's (1887) fluids, or the fixative of Sanfelice (1918). The material fixed in Newcomer's or Carnoy's fluids was stained by the acetic-orcein squash technique (La Cour, 1941), and reproductive tissues fixed in Sanfelice's fluid were sectioned at either 8 or 10 micra and stained with Newton's (1926) crystal violet. All observations were made on meiotic cells of spermatogenesis (except in *Herviella mietta*, where spermatogonial cells were also studied) with a Nikon (Nippon Kogaku) microscope equipped with a 100✕ (n.a. 1.25) oil immersion objective and 10✕, 20✕, and 30✕ oculars. Drawings were made with the aid of a

camera lucida and reproduced at a table-top magnification of 4260✕.

OBSERVATIONS

1. *Dendrodoris nigra* (Fig. 10). The five individuals of this species on which we were able to obtain satisfactory observations all had 13 bivalents during prophase of the first meiotic division.

2. *Herviella mietta* (Fig. 11). Only one specimen of this species gave satisfactory results. It had 13 bivalents during diakinesis and 26 chromosomes during metaphase in spermatogonial cells.

3. *Dolabrifera dolabrifera* (Figs. 12 and 13). Nine specimens had meiotic cells that were satisfactory for chromosome number determinations. All had 17 bivalents during Prophase I and Metaphase I. The chromosomes of a cell during diakinesis from an acetic-orcein squash preparation are shown in Figure 12. Metaphase I bivalents from a cell of paraffin sectioned material are shown in Figure 13.
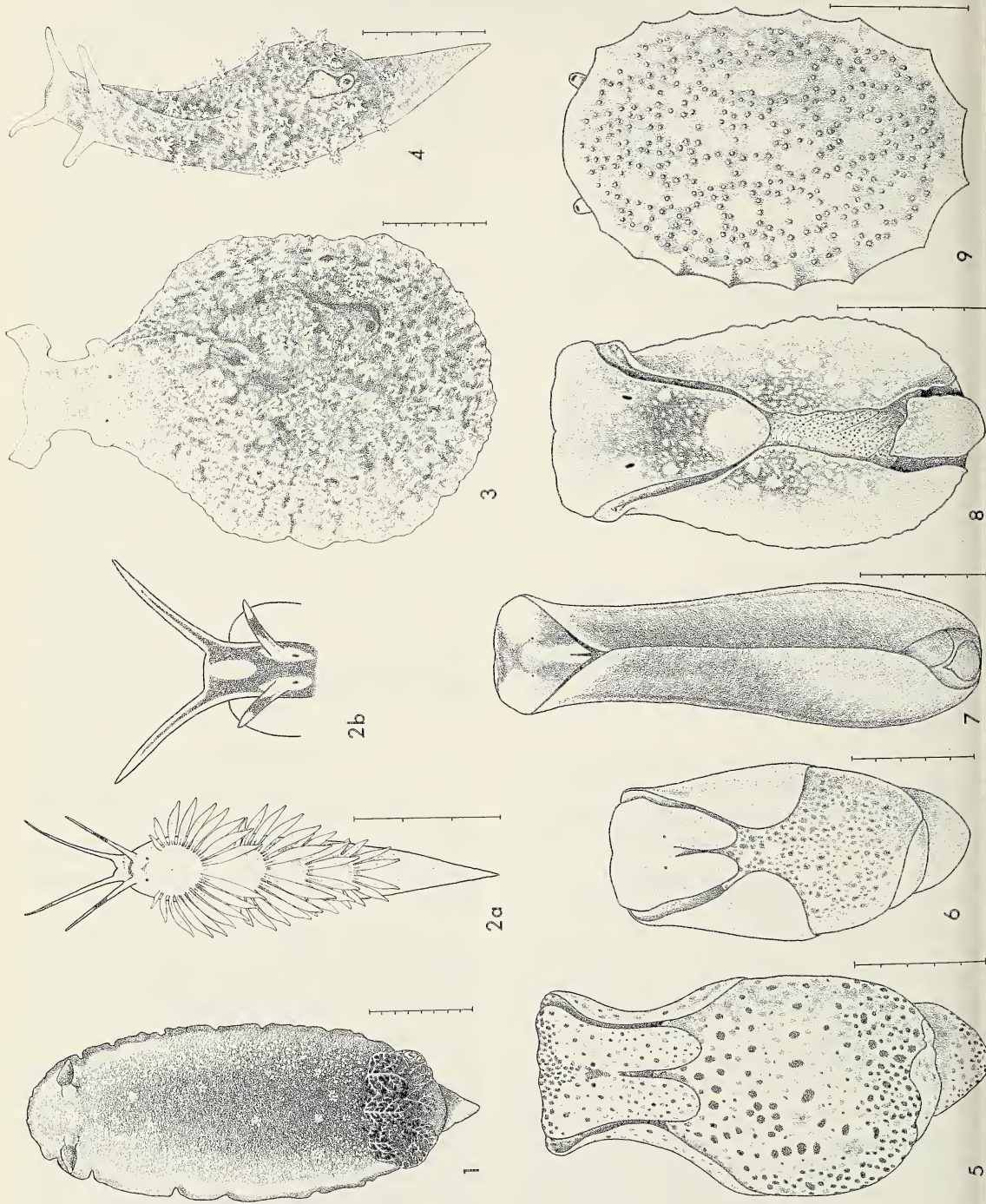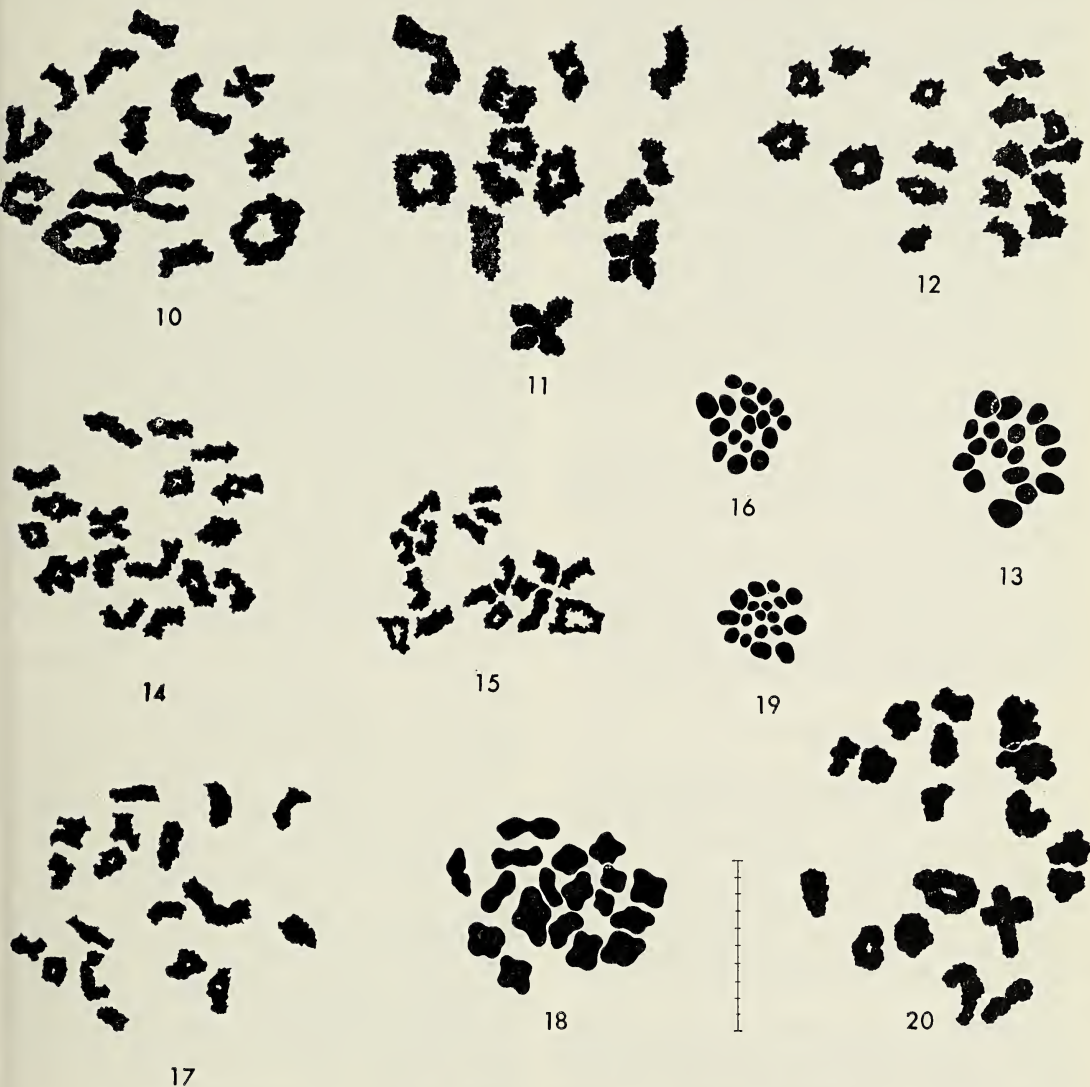
Figs. 10–20. Chromosomes of Eniwetok opisthobranchs. *10, Dendrodoris nigra. 11, Herviella mietta. 12 and 13, Dolabrifera dolabrifera. 14, Stylocheilus longicauda. 15, Haminoea musetta. 16, H. linda. 17, Lathophthalmus smaragdinus. 18, Smaragdinella calyculata. 19 and 20, Onchidella evelinae.*
Figs. *10–12, 14, 15, 17,* and *20* are of male diakinesis bivalents; *13, 16, 18,* and *19* are of male Metaphase I bivalents. Figs. *10–12, 14, 15, 17, 18,* and *20* are from acetic-orcein squash preparations; *13, 16,* and *19* are from sectioned material stained with crystal violet. Measurement line divided into micra.

Figs. 1–9. Eniwetok opisthobranchs used in this study. *1, Dendrodoris nigra. 2, Herviella mietta. 3, Dolabrifera dolabrifera. 4, Stylocheilus longicauda. 5, Haminoea linda. 6, H. musetta. 7, Lathophthalmus smaragdinus. 8, Smaragdinella calyculata. 9, Onchidella evelinae.* Measurement lines are divided into millimeters.

4. *Stylocheilus longicauda* (Fig. 14). Satisfactory results were obtained from two specimens. Both had 17 bivalents during diakinesis.

5. *Haminoea linda* (Fig. 16). We were able to obtain cells that were satisfactory for study from only one specimen. These cells had 17 bivalents during Metaphase I.

6. *Haminoea musetta* (Fig. 15). The two specimens studied both had 17 bivalents in cells at the diakinesis stage. The diakinesis bivalents of one such cell are shown in Figure 15.

7. *Lathophthalmus smaragdinus* (Fig. 17). Two specimens had meiotic cells that were satisfactory for chromosome number determinations. All dividing cells from which accurate counts could be made had 18 bivalents.

8. *Smaragdinella calyculata* (Fig. 18). Satisfactory results were obtained from two specimens. Both had 18 bivalents during diakinesis and Metaphase I.

9. *Onchidella evelinae* (Figs. 19 and 20). The two individuals on which we were able to obtain satisfactory observations both had 18 bivalents during diakinesis and Metaphase I.

DISCUSSION

The chromosome numbers of the eight genera of opisthobranchiate mollusks presented here add to the information previously obtained by reliable authors. Of the species studied five belong to three families not studied in past reports, i.e., the Favorinidae (Nudibranchia), and the Atyidae and Smaragdinellidae (Cephalaspidea).

Dendrodoris nigra (Nudibranchia, Dendrodorididae) was studied previously by Inaba and Hirota (1958). We found the same number of chromosomes (n=13) for this species from Eniwetok as they reported it to have from Japan. *Herviella mietta* (Nudibranchia, Favorinidae) from Eniwetok also had a haploid number of 13, which adds to the growing information regarding the extreme conservativeness of chromosome numbers of most opisthobranchs. All 16 species of nudibranchs (belonging to nine different families) studied so far have this same haploid number, n=13.

Among the Cephalaspidea three species have been studied previously (Inaba, 1959a and personal communication), each belonging to a dif-

ferent family. Each of these three species had a haploid number of 17. In the present investigation two species from each of two additional families were studied. *Haminoea linda* and *H. musetta* (Bullacea, Atyidae) had a haploid chromosome number of 17, but *Smaragdinella calyculata* and *Lathophthalmus smaragdinus* (Philinacea, Smaragdinellidae) each had the haploid number 18. It will be interesting to see if species of the other families of the Philinacea (the Philinidae, Scaphandridae, Aglajidae, Gastropteridae, and Runcinidae) also have 18 pairs of chromosomes. If so, this would separate this superfamily from all other cephalaspideids and, additionally, from all other cytologically known entomotaenids and anaspideids and from most of the sacoglossans. The haploid number 18 in this group may have another significance in that it seems to strengthen Pelseneer's (1893) and Boettger's (1955) views regarding the origin of the Basommatophora from the Cephalaspidea, since the haploid number 18 is basic for the Basommatophora.

Dolabrifera dolabrifera and *Stylocheilus longicauda* (Anaspidea, Aplysiidae) both had the haploid number 17, as did the two species studied from this family by Inaba (1959a).

Onchidella evelinae (Soleolifera, Onchidiidae) had a haploid number of 18, which is one bivalent more than that reported by Inaba (1961a) for *O. kurodai* of the same genus from Japan, but n=18 is the same number reported by Natarajan (1959) for *Onchidium verraculatum* from India. Much more cytological information is desirable for the various species belonging to this aberrant order, which is sometimes placed with the "pulmonates" (e.g., Baker, 1955).

The conservativeness of chromosome number in the opisthobranchs indicates that these mollusks are extremely resistant to changes in chromosome numbers, regardless of major evolved morphological diversities within the various groups, and that certain major divisions (i.e., the Nudibranchia and the orders with n=17 and higher chromosome numbers) have probably been separated for an extremely long geological time. In this regard, *Bosellia mimetica* is either an extremely aberrant species, or its cytological evolution has been much more rapid than has been the evolution of its gross

morphology in respect to all other opistho-branchs so far studied.

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Observations on the Biology of the Lousefish,
Phtheirichthys lineatus (Menzies)

Donald W. Strasburg[1]

THE LOUSEFISH, *Phtheirichthys lineatus* (Menzies), is a slender member of the Echeneidae which is often free-swimming but which also attaches to immotile objects or slow-swimming fishes. It is pantropical, uncommon, and little known biologically.

This paper reports on 24 lousefish in the collections of the Bureau of Commercial Fisheries Biological Laboratory in Honolulu. Capture data for these specimens are presented in Table 1. Most of the other data were derived from preserved fish with the exception of one 256-mm specimen which was maintained alive in a swimming pool for several weeks.

Mr. Richard D. Samuels and Mr. Richard N. Uchida captured the fish, Mr. Everet C. Jones identified many of the food items, and Mr. Tamotsu Nakata prepared the figure. All are employees of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

COMMON NAME

The American Fisheries Society (1960:48) lists the common name of *Phtheirichthys lineatus* as "slender suckerfish." *P. lineatus* is an uncommon or rare fish, however, and no one of my acquaintance applies this rather arbitrary name to it. In Honolulu, *Phtheirichthys* is usually called "lousefish," a name used earlier by Jordan (1907:680). "Lousefish" is used throughout this report.

ATTACHMENT

The data in Table 1 were grouped to reflect the various objects to which lousefish attached. Most small fish (ca. 40–130 mm standard length) came from essentially motionless objects: buoys, baits, and large dead fish hanging

from the longline gear that caught them. One lousefish was attached to a living porcupinefish, *Diodon hystrix* Linnaeus, a notoriously slow swimmer. Lousefish have been reported from other slow swimmers including turtles (Menzies, 1791:187), barracuda (Jordan and Evermann, 1898:2268; Schultz, 1943:256; Smith, 1950:341), and large groupers (Smith, 1950: 341). It is difficult to accept Jordan and Evermann's statement (1898:2268) that lousefish occur on spearfishes.

Six specimens were free-swimming when collected, including the three largest ones which were attracted to a submerged light at night. One of the latter was kept alive in the ship's baitwell for 10 days, during which time it was occasionally seen to attach to the tank walls for 1 or 2 seconds at a time. Later it was transferred to a circular plastic swimming pool, 23 ft in diameter and 4 ft deep, which was supplied with running salt water. Here its attaching and other behavior were observed for two 1-hr periods each day for 25 days.

The captive lousefish attached only under two conditions: when I entered the pool or when it had been fed to satiety. It was necessary to clean the pool's windows and drain-strainers every few days; when I entered the water to do this work, the fish abruptly ceased swimming and attached to the pool's bottom or side. It usually remained attached for a few minutes and then darted toward me, especially if I was swimming. When I swam, it accompanied me around the pool, staying about 1 ft from my bare feet, but making no effort to attach to me.

The lousefish was fed once or twice a day. Feeding was avid to the point of greediness, the satiated fish having a bulging belly and cheeks, and usually being unable to close its mouth. In this state its swimming movements appeared to be hampered. It sank to the pool's bottom and did one of three things: either it swam slowly back and forth with a great deal

TABLE 1

CAPTURE DATA FOR *Phtheirichthys lineatus*

DATE	LATITUDE	LONGITUDE	SEX*	STANDARD LENGTH (mm)	HOST OR HABIT
2/ 1/57	13°44′ S	110°02′ W	?	55.7	dip-netted beneath night-light
10/ 5/62	19°12′ N	156°05′ W	–	256	dip-netted beneath night-light
10/ 5/62	19°12′ N	156°05′ W	M	273	dip-netted beneath night-light
9/29/51	21°24′ N	158°15′ W	F	300	dip-netted beneath night-light
10/30/58	04°58′ S	149°52′ W	?	32.8	caught by British Columbia trawl
11/ 1/58	05°00′ S	149°58′ W	?	48.4	caught by British Columbia trawl
8/28/56	11°23′ S	134°32′ W	?	46.0	in *Thunnus albacares* stomach
7/18/50	03°00′ S	171°22′ W	?	53.0	attached to longline buoy
7/20/60	11°30′ N	161°21′ E	?	53.2	attached to longline buoy
8/26/56	13°26′ S	132°16′ W	?	54.0	attached to longline buoy
7/18/50	03°00′ S	171°22′ W	?	56.1	attached to longline buoy
2/ 7/63	17°57′ N	149°39′ W	?	51.3	attached to longline bait (squid)
2/23/63	20°41′ N	150°06′ W	?	55.5	attached to longline bait (squid)
2/ 7/63	17°57′ N	149°39′ W	?	58.9	attached to longline bait (squid)
7/31/63	21°24′ N	149°51′ W	?	61.6	attached to longline bait (squid)
2/ 6/63	18°16′ N	149°46′ W	?	92.4	attached to longline bait (squid)
8/27/56	12°16′ S	133°20′ W	?	44.0	attached to longline bait (fish)
7/24/63	14°22′ N	149°58′ W	–	81.3	attached to longline bait (fish)
7/10/63	14°24′ N	150°11′ W	–	112	attached to longline bait (fish)
5/ 5/62	02°09′ N	157°13′ W	?	48.9	attached to dead *Thunnus albacares*
2/ 6/63	18°16′ N	149°46′ W	F	126	attached to dead *Coryphaena equiselis*
8/29/62	Kahana Bay, Oahu		?	59.6	attached to living *Diodon hystrix*
7/18/50	03°00′ S	171°22′ W	?	48.6	unknown
3/15/59	14°49′ N	150°12′ W	?	60.2	unknown

* (?) = sex could not be determined; (–) = specimen not dissected.

of lateral wriggling, or it rested on the bottom with its belly down, or it attached to the pool's bottom or side. Each of these activities lasted as long as 15–20 minutes and appeared to represent a post-gorging rest. Sometimes the stuffed fish would regurgitate part of its meal and revert to swimming. Although bottom-resting was the most common post-feeding act, it is unlikely that this could happen in nature because substrates suitable for resting would not be available. If satiation resulted in such a temporary weight gain or such a loss of swimming mobility that a resting place was necessary, it is probable that a wild fish would never venture far from its attachment site. It is also probable that full meals are rare in the wild.

The lousefish made no use of its fins when resting on the bottom or attached. The large caudal was collapsed about its long central rays, the dorsal and anal were folded against the body, the pelvics were depressed, and the pectorals were semiflexed.

SWIMMING

Except for the situations noted above, the captive lousefish swam constantly in either of two patterns. More commonly it swam back and forth across the pool, passing near the center each time. In a round trip, one passage was at the pool's mid-depth (2 ft) and the return just above the bottom (4-ft depth). On the mid-depth trip the fish's attitude was normal (disk up); on the bottom trip it was inverted (disk down). During the short vertical connecting trips, the disk faced the tank walls. The fish oriented to the walls or bottom when 6–12 inches from them. Less commonly it circuited the pool's periphery on its side, with the disk facing the pool wall.

Some differences in swimming method were noted within these patterns. When the fish was swimming with the disk up, the head was essentially horizontal, the body axis hung about 8° below the horizontal, and the pectorals were

well extended. When it swam inverted, the head was again horizontal and the trunk axis dipped about 8° below the horizontal, but the caudal fin touched the pool bottom and the pectoral fins were folded. When it swam on its side along the wall, the pectorals were half folded but the caudal did not touch the wall. The inverted fish kept its head about 1½ inches above the bottom, but when swimming on its side 2 or 3 inches separated the head and the wall.

In most swimming the caudal fin was well expanded to a rhomboidal or oval shape, the pelvics were folded, and the dorsal and anal fins were only partly erect. The fish's sinuousity was impressive, as it could execute 180° turns in a circle about 6 inches in diameter. The pectorals and sometimes the pelvics were erected when the fish changed course or its plane of swimming, and also when it had just been fed to satiation. In addition, the gorged fish occasionally swam at an angle of 15° to 35° from the horizontal.

Swimming speeds were calculated for each of the three swimming attitudes and for the hungry and fed fish. Data were obtained by timing the fish as it swam between reference points on the pool's sides. Speed data are given in Table 2. In contrast to normal and inverted swimming, side-swimming when satiated was observed only once. The values given are the extremes of a number of readings. The loss of speed after feeding was marked but of short duration. Unfortunately, the only data showing this change relate to tail-beat frequency, not to speed. Tail beats were counted at 66/minute immediately after feeding, but suddenly increased to 78 and 84 beats/minute 11 minutes later.

TABLE 2

Swimming Speed for the Lousefish

STATE OF FISH	SWIMMING ATTITUDE	RANGE IN SWIMMING SPEED (ft/sec)
Not fed for 7–12 hr	normal	1.61–2.05
	inverted	1.88–2.04
	on side	1.41–2.21
Fed to satiety	normal	0.80–1.61
	inverted	0.87–1.32
	on side	1.15–1.39
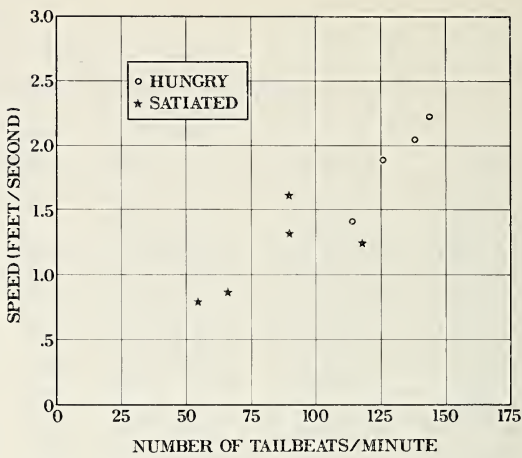
Fig. 1. Speed versus tail-beat frequency in the lousefish.

Figure 1 shows the relation between speed and tail-beat frequency. Speed and tail-beat data were obtained simultaneously as the fish transited the pool. The number of beats per minute ranged from 48 to 144. No speed estimate was obtained for the 48-beat value, which occurred 2 minutes after gorging and 1 minute before the fish sat on the bottom.

RESPIRATION

While the lousefish was swimming, its mouth was always open and no opercular movements were detectable. In this respect it resembled *Remora remora* (Linnaeus), which ceased opercular pumping under conditions of optimum, if artificial, water flow over the gills (Strasburg, 1957). The speed range (or the flow rate) observed for the hungry lousefish (1.41–2.21 ft/sec), however, was more than twice the range (0.75–0.88 ft/sec) judged optimal for *R. remora* (Strasburg, 1957).

When gorged, the lousefish usually sat on the bottom or attached. Its mouth remained open and opercular respiratory movements were conspicuous. The well-developed tongue was alternately pressed to the mouth's roof and returned to its bed, in a rhythm keyed to the opercular movements. Sometimes the fish oriented to face the weak current at the pool's inlet. The number of respirations per minute ranged from 84 to 120—a much lower range than for *R. remora*, which had from 203 to 244 respirations per

minute when attached but unfed (Strasburg, 1957). Stuffing the digestive tract with food possibly inhibits the respiratory rate on some mechanical basis. Once when the lousefish fed until it bulged, and then attached to the bottom, it had a rate of 84 respirations per minute. Six minutes later, when it regurgitated four cubes of shark flesh, the rate increased to 114 respirations per minute.

FOOD AND FEEDING

The results of stomach analyses of four lousefish were presented in an earlier paper (Strasburg, 1959:246). It has since been possible to examine 16 more stomachs and obtain better definition of the scope of the diet, and also to observe the feeding behavior of a living specimen.

Of the 20 lousefish stomachs examined 2 were empty. The balance contained mostly planktonic crustaceans, especially small and larval forms. The crustaceans and the number of stomachs in which they occurred were as follows: hyperiid amphipods (1), unidentified amphipods (6), crab larvae (2), unidentified decapod larvae (1), stomatopod larvae (2), Euphausiacea (1), Mysidacea (1), Ostracoda (3), unidentified crustacean fragments (3), and the following copepods: *Candacia pachydactyla* (5), *C. aethiopica* (2), *Candacia* sp. (1), *Scolecithrix danae* (1), *Euchaeta* sp. (3), unidentified calanoids (3), *Sapphirina* sp. (1), *Oncaea* sp. (1), and unidentified cyclopoids (1). Also, 2 stomachs contained fish flesh and bones, and 2 had small flakes of rusty iron.

None of the food species is parasitic, and it is thus unlikely that the lousefish is a cleaner, in contrast to most other echeneids (Szidat and Nani, 1951:413; Maul, 1956:14; Strasburg, 1959:246). Instead, it appears to feed rather selectively on planktonic animals, especially on such conspicuous creatures as the black-and-white copepods *Candacia pachydactyla* and *C. aethiopica,* the iridescent blue copepod *Sapphirina,* and large stomatopod larvae. Rust flakes from the fishing vessel probably were ingested because they were relatively conspicuous. Mysids had been eaten only by the 59.6-mm lousefish attached to a living *Diodon hystrix* caught in Kahana Bay, Oahu. Mysids abound in this shallow bay, and the fish had gorged on 41 of them.

The captive lousefish was fed small cubes of bread, shrimp, or shark flesh once or twice a day. Presentation of food was preceded by a cue (described below) and continued until the offerings were ignored. The fish reacted to food particles from a distance of about 3 ft; the water was very clear. It refused particles lying on the bottom, and preferred to feed on sinking food pieces near the surface. Pieces less than about 3 mm in greatest dimension were ignored in favor of larger ones (up to about 1 cm in greatest dimension). The 3-millimeter pieces were "inhaled" without noticeable jaw movements, whereas those in the 7- to 10-mm range were gulped with conspicuous jaw action. As noted earlier, the fish was a greedy feeder and ate until its belly and cheeks bulged. A full meal required 3 or 4 minutes to consume. When fed once a day for 3 successive days, the volume of shark flesh eaten per meal was 5.1, 5.0, and 2.6 cc. On the last day the fish also ate bread crumbs whose volume had not been measured.

The lousefish was accidentally placed in the wrong pool at first, and for a time I planned to recapture it by dip net for transfer elsewhere. It was necessary to condition the fish to the dip net, for its earlier capture had made it wary. A dip net was placed in the pool before each feeding, and food was offered over the net so that the fish had to swim above the meshes to feed. On the third day of this procedure (the fifth feeding) the fish swam slowly but directly to the net when it was placed in the pool. At the next feeding it dashed immediately to the net, and continued to do so whenever the net was shown. Because it proved unnecessary to transfer the fish, this conditioning went for nought. The fish was subsequently trained to come to the feeding area when the water's surface was slapped with the hand.

COLOR AND COLOR CHANGE

A description of the life colors of the lousefish could not be found in the literature and is therefore presented here. In sunlight the dorsal surfaces of the head and body are navy blue and the ventral surfaces are white. In shade the

navy blue often appears as velvety black. Separating these contrasting colors are three lengthwise stripes along the sides. The upper stripe is narrow and light blue, the middle is broad and black, and the lower is narrow and silvery white. The light-blue stripe commences on the upper snout (where it meets its fellow), touches the upper edge of the eye, and continues thence to the caudal base. The black stripe runs from the snout through the eye to the caudal base, and expands on the caudal fin so that the fin is black except for narrow white dorsal and ventral margins. The silvery-white stripe runs from the rictus to the lower edge of the eye and thence along the lower mid-side to the caudal base. The dorsal and anal fins are black basally and margined with white anteriorly. The pectorals and pelvics are plain blackish.

This color was characteristic of the captive lousefish during its first 7 days in the swimming pool. Thenceforth its ventral surface gradually darkened, changing from white to gray-spotted (eighth day) to uniform gray (ninth day) to gray-black (tenth day). Subsequently the color of its undersides fluctuated between gray, deep slate blue, and black, there being no apparent relation between color and incident light or fish activity. Frequently, however, the color of the undersides was lighter just after feeding. Sometimes the back and the base of the dorsal and anal fins were the same color as the undersides. The three lateral stripes were unvaryingly the same. By the twenty-first day the fish's dorsal and ventral surfaces were both jet black, and no further changes were observed. When the fish was preserved after 25 days, it retained its melanistic coloration in alcohol.

During the lousefish's 25-day confinement, the color of the pool walls changed markedly as the diatom *Melosira* proliferated from essentially nothing to a growth 2 inches thick. The fish's gradual color change paralleled this growth. The darkening may have been caused by a general increase in the amount of melanin. On the other hand, a faculty for rapid color change has been reported for *Echeneis naucrates* (Beebe and Tee-Van, 1933:222; Nichols *in* LaGorce, 1939:163; Sanborn, 1932:89; Townsend, 1927:171) and for *Remora remora* (Maul, 1956:50, 66), and thus it is possible

that the observed changes were highly transitory.

Another explanation for this color change derives from observations on echeneids which regularly attach. These fish have been stated either to lack countershading (Cott, 1940:43; Pincher, 1948:283) or to have reversed countershading (Norman and Fraser, 1949:176). A lack of countershading supposedly results from a failure to maintain constant orientation to a light source; a reversal of countershading arises from the fact that the echeneid's belly is usually more brightly illuminated than its back. The first explanation possibly fits the color change described above for the lousefish. When captured it had normal countershading, but began to lose it after a period in which swimming was often inverted or on the side. When free in the pelagic environment the lousefish presumably swims in a normal attitude.

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The Planktonic Shrimp, *Lucifer chacei* sp. nov., (Sergestidae: Luciferinae), the Pacific Twin of the Atlantic *Lucifer faxoni*

Thomas E. Bowman[1]

ABSTRACT: *Lucifer chacei* sp. nov., closely related to the Atlantic *L. faxoni* and identified as the latter species by previous authors, is described and compared with *L. faxoni*. It is widely distributed in the tropical Pacific, and like *L. faxoni* inhabits coastal waters.

THE PLANKTONIC SHRIMP genus *Lucifer* (family Sergestidae) contains six currently recognized species, of which all have been reported from the Indo-Pacific, but only two, *L. typus* Milne Edwards and *L. faxoni* Borradaile, are known to occur in the Atlantic. An unpublished study which I recently completed on the distribution of the two Atlantic species off the southeastern coast of the United States shows that *L. faxoni* is essentially a coastal species. Since coastal plankters more often than not are restricted to one ocean, or even to a single coast of one ocean, it seemed advisable to re-examine the evidence for the occurrence in the Indo-Pacific of *L. faxoni,* the type locality of which is in the Atlantic, off Chesapeake Bay (restricted by Holthuis, 1959).

For this study Atlantic specimens of *L. faxoni* from Bloody Bay, Tobago, West Indies, were compared with Pacific specimens of *Lucifer* from Eniwetok, Marshall Islands, and from several of the Society Islands. Both Atlantic and Pacific specimens key out to *L. faxoni* in Hansen (1919), but they are specifically distinct, and a new species is established herein for the Pacific form.

Surprisingly, the common short-eyestalked Atlantic species, *L. faxoni,* has never been described and illustrated adequately (Hansen's drawings of *L. faxoni* in his 1919 monograph are actually of the new Pacific species); hence illustrations of taxonomically important features of *L. faxoni* are given herein.

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Lucifer chacei, new species
    Figs. 1–4

Lucifer faxoni Borradaile.—Hansen, 1919: 61–63, pl. 5, figs. 3a–3i.—Edmondson, 1925:5.—Hiatt, 1947:241–242.—Chace, 1955:4.

Leucifer reynaudi H. Milne Edwards.—Edmondson, 1923:35.

MATERIAL EXAMINED: MARSHALL ISLANDS: Eniwetok Atoll; lagoon, 4.8 km west of Parry I., net tow at depth of approximately 3 m, 26–27 July 1960, 2435–0800 hours, by Woods Hole Oceanographic Institution, ♂ holotype (USNM 113327), ♀ allotype (USNM 113328) and 55 paratypes. Rongelap Atoll; 1 km off Yugui I., depth of water 24 m, dip net under night light, 30 July 1946, by Earl S. Herald, 3 ♂, in poor condition, reported as *L. faxoni* by Chace (1955). TUAMOTU ISLANDS: Tikahau Atoll; lagoon, south of deep water pass, net tow at depth of approximately 4 m, 12 April 1957, 2015–2030 hours, station 19 of Smithsonian Bredin 1957 Expedition, 43 specimens. SOCIETY ISLANDS (Smithsonian-Bredin 1957 Expedition stations): Tahiti: Papeete Harbor, dip net under night light, 4 May, 2100–2130 hours, station 99, 40+ specimens. Moorea: Opunohu Bay, east side, net tows, 9 May, 1530 hours, station 114, 43 juveniles. Bora Bora: East of Farepiti Point, dip net under night light, 24 April, 2000–2030 hours, station 52, 50+ specimens; off Teraia Point, depth of water 30 m, net tows, 25 April, 0900–1100 hours, station 55, 24 specimens; west of north end of Toopua I., depth of water 13 m, dip net under light, 25 April, 2030–2100 hours, station 63, 30+ specimens.

FIG. 1. *Lucifer chacei: a,* female, lateral; *b,* anterior end of male head, lateral; *c,* anterior end of female head, lateral; *d,* anterior end of male head, dorsal; *e,* male posterior head and anterior pereon, lateral; *f,* female uropod and telson, lateral; *g,* male telson, lateral; *h,* female telson, lateral; *i,* male telson, dorsal; *j,* apex of male telson, dorsal.
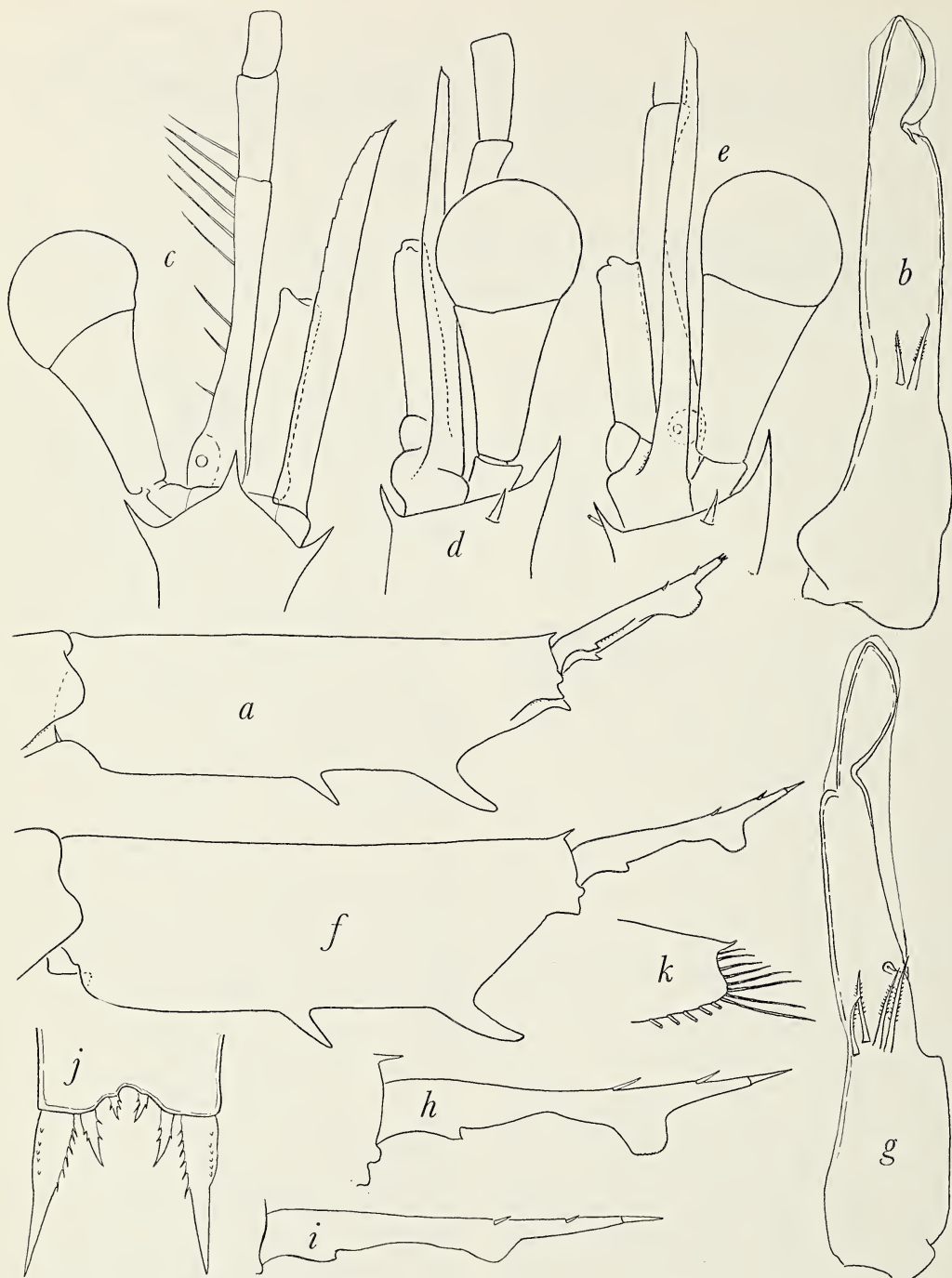
FIG. 2.   a–b, Lucifer chacei: a, male 6th abdominal somite and telson, lateral; b, endopod of left male 2nd pleopod, anterior. c–k, Lucifer faxoni: c, anterior end of male head, dorsal; d, same, lateral; e, anterior end of female head, lateral; f, male 6th abdominal somite and telson, lateral; g, endopod of left male 2nd pleopod, anterior; h, male telson, lateral; i, immature male telson, lateral; j, apex of male telson, dorsal; k, apex of exopod of male uropod, dorsal.
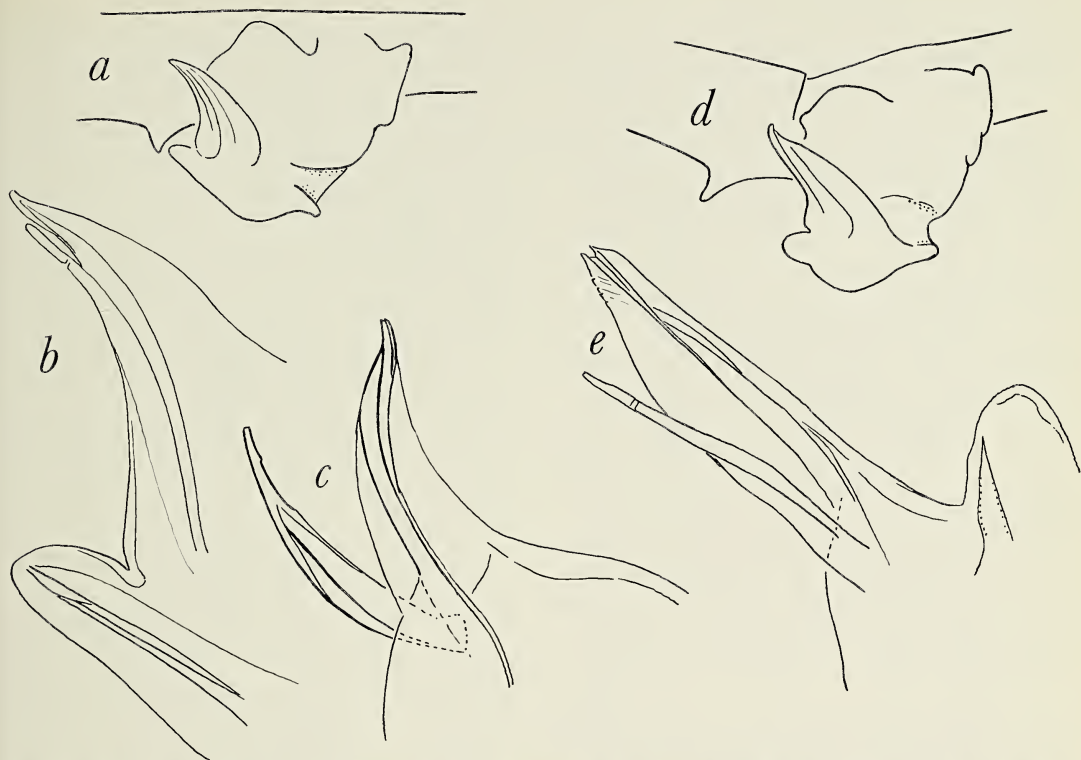
FIG. 3.   *a–c, Lucifer chacei*: *a,* petasma *in situ*, medial; *b,* petasma sheath with its processus ventralis, and proximal lobe at base of sheath; *c,* petasma sheath of another male, with processus ventralis displaced. *d–e, Lucifer faxoni*: *d,* petasma *in situ*, medial; *e,* petasma sheath with processus ventralis displaced.

DIAGNOSIS: A Pacific species belonging to Hansen's (1919) "Group B" (species with short eyestalks), closely resembling the western Atlantic *L. faxoni* in having the apex of the petasma acute, without transverse lines or protruding plates or scabrousness, and in having a slender processus ventralis with acute apex.

The diagnostic features of *L. chacei* in comparison with *L. faxoni* are shown in Table 1.

The new species is named for my colleague, Fenner A. Chace, Jr., in recognition of his many contributions to decapod crustacean taxonomy.

REMARKS: Of the remaining species of *Lucifer*, only *L. hanseni* Nobili agrees with *L. faxoni* and *L. chacei* in having a slender, acutely ending processus ventralis. However, *L. hanseni* can be identified immediately by the uniquely shaped uropodal exopod, in which the outer tooth is located considerably proximad of the distal margin.

Previous workers reporting *L. faxoni* from the Pacific naturally based their identifications on Hansen's (1919) monograph. None had reason to suspect that Hansen's description and illustrations dealt with an undescribed species. Although Hansen stated that the Copenhagen Museum possessed several samples of Atlantic *L. faxoni,* he could not have compared them carefully with his Siboga material. I cannot believe that the distinguished Danish carcinologist would have overlooked the differences separating the two species.

L. chacei is so similar to *L. faxoni* that it is possible that their genetic divergence is at the subspecific rather than the specific level. They probably have been derived from a common ancestor. The actual level of divergence from this ancestor cannot be ascertained from available collections, and, since the two forms are completely isolated from one another, there is no possibility of gene flow between them at present. If plans for a sea level canal connecting the Caribbean Sea and the Pacific Ocean are carried out, the picture may change drastically.

Fig. 4. *Lucifer chacei*, female, thelycum: *a,* ventral, *b,* lateral. *A, P,* Anterior and posterior margins of ventral process; *P3,* base of 3rd pereopod; *SP,* spermatophore; *ATR,* atrium; *SEM. REC.,* seminal receptacle.

DISTRIBUTION OF *L. chacei*: EAST INDIES: many localities (Hansen, 1919). HAWAIIAN IS-LANDS: Oahu, Molokai (Hiatt, 1947). LINE IS-LANDS: Fanning Island (Edmondson, 1923). TUAMOTU ISLANDS: Tikahau Atoll. SOCIETY IS-LANDS: Tahiti (Papeete Harbor); Moorea (Paopao Bay); Bora Bora (south of Farepiti Pt., off Tereia Pt., west of Toopua I.). MAR-SHALL ISLANDS: Rongelap Atoll (off Yugui I.); Eniwetok Atoll (west of Parry I.). It is probably widespread in the tropical Pacific, and, like its Atlantic counterpart, *L. faxoni*, is prob-ably a coastal species. Along the east coast of Australia it is replaced by *L. penicillifer* Han-sen (Gordon, 1956).

REPRODUCTION: I have examined the female

TABLE 1

DIAGNOSTIC FEATURES OF *L. chacei* COMPARED WITH *L. faxoni*

Lucifer chacei, NEW SPECIES	*Lucifer faxoni* BORRADAILE
1. Last segment of peduncle of ant. 2 in ♂ reaches beyond eye and nearly to distal margin of 1st segment of ant. 1 peduncle, in ♀ reaches beyond middle of cornea and to distal third of 1st seg-ment of ant. 1 peduncle.	1. Last segment of peduncle of ant. 2 in ♂ reaches middle of cornea and distal third of 1st segment of ant. 1 peduncle, in ♀ reaches proximal margin of cornea and to distal third of 1st segment of ant. 1 peduncle.
2. Rostrum reaches proximal border of statocyst.	2. Rostrum reaches almost to distal end of statocyst.
3. Ventral cushion of ♂ telson much broader than its posterior height.	3. Ventral cushion of ♂ telson about as broad as its posterior height.
4. Sheath of petasma curved.	4. Sheath of petasma straight.

external reproductive system in specimens cleared in lactic acid. The thelycum consists of a conical median ventral process between the bases of the third pereopods, behind which is a longitudinal slit leading into the atrium, a sclerotized pouch formed by a median depression of the sternum. When present, the spermatophore neck is inserted into the atrium through the slit. The large paired seminal receptacles lie posterior and lateral to the atrium. In my cleared material it was evident that the seminal receptacles connect by ducts to the atrium, but the nature of the ducts was not clear. I could not detect the female genital openings, which Burkenroad (1934) and Gordon (1956) found on the coxae of the third pereopods. The entire system is rather complex and, as Gordon pointed out, is in need of critical study using histological techniques.

Several females from Bora Bora had clusters of eggs attached by short stalks to the ischia of the third pereopods. The eggs were probably about ready to hatch, for well-developed nauplii could be seen through the egg membranes. Because of the ease with which eggs become detached from the third pereopods in preserved specimens, Gordon (1956) doubts that they stay attached until the nauplii emerge, a period of more than 36 hours according to Brooks (1882). The Bora Bora specimens prove that at least some of the eggs remain attached until eclosion.

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Revision of the Genus *Pandanus* Stickman, Part 21
The *Pandanus monticola* Group in Queensland, Australia

HAROLD ST. JOHN[1]

IN AUSTRALIA the section *Acrostigma* of the genus *Pandanus* occurs only in the rain forests of eastern Queensland. The first known species there was *P. monticola* F. Muell. It is here given a full description and illustrations, as is one new species segregated from it.

Section *Acrostigma*

Pandanus monticola F. Muell. (sect. *Acrostigma*), Fragm. Phytog. Austral. 5:42, 1865; 7:63, 1870; 8:220, 1874; Martelli, Webbia 4(2):pl. 30, fig. 21–27, 1914

Figs. 232–234

DESCRIPTION (from St. John 26,237): Shrubs 1–3 m tall, simple, erect or decumbent; stem 25–40 mm in diameter, yellowish, unarmed, bearing in a terminal plume the arching leaves 1.8–2.18 m long, 4 cm wide near the base, 4.2 cm wide at the middle, subcoriaceous, ligulate, gradually long tapering to a subulate tip which 10 cm down is 7 mm wide, the very base unarmed and amplexicaul but beginning 5 cm up the margins with spines 1.5–2 mm long, 1.5–5 mm apart, the lowest ascending but the others salient, subulate, stramineous; the nearby midrib with prickles 0.5–0.8 mm long, 1.5–6 mm apart, the base thick like a boss, the apex reflexed and subulate-conic; at the midsection the margins with prickles 0.5–0.9 mm long, 2–5 mm apart, subulate, appressed ascending; the nearby midrib unarmed; near the tip the margins and midrib below with the teeth 0.3–0.5 mm long, 1–3 mm apart, subulate-serrate, ascending, above the two pleats with teeth 0.5–0.7 mm long, similar but broader-based and occasionally double; pistillate inflorescence terminal, erect, 2-headed, the upper syncarp larger, but with a small, secon-

dary, subterminal one below; peduncle 50 cm long, 1 cm in diameter, trigonous, leafy bracted, the middle bracts 65 cm long, 3.4 cm wide; the larger syncarp 9.5 cm long, 7.5 cm in diameter, ovoid, bearing very numerous drupes, these 24–28 mm long, 2–3 mm wide, 1.5–2.5 mm thick, yellow, narrowly lance-subulate, 4–6-angled, upper ¾ free; pileus 13–14 mm long, subulate, sharply angled on drying, the surface smooth, the tip curved toward the apex of the syncarp; style 6–8 mm long, subulate, cartilaginous, yellowish, smooth, arcuate; stigma distal, 5–6 mm long, linear, brown; endocarp in lower ninth, 4–6 mm long, cartilaginous, yellowish, the walls 0.1 mm thick; seeds 4 mm long, broad oblong-ellipsoid; apical mesocarp with a central core of fibers and with fleshy sides; basal mesocarp very small, fibrous and fleshy.

HOLOTYPE: Australia, Rockingham's Bay proximis (staminate only), (MEL), specimen examined! This was published as "montibus sinu Rockingham's Bay proximis." Isotype (K)! In the Paris herbarium there is an original collection, with part of a leaf and half of a syncarp, that is a far better specimen than the holotype preserved in Melbourne. It was distributed by von Mueller in 1874, and the data is in his handwriting: "Rockingham's Bay, on mountains, most probably this belongs to *P. monticola*, of which I had no flowers, when I described it, fruit small, bracts white." (P)!

SPECIMENS EXAMINED: Queensland, without locality, *L. J. Brass 2,128* (A); in valle Dalrympli, 22 Oct. 1864, *J. Dallachy* (MEL); Russell River, *F. von Mueller* (MEL); Mt. Bellenden-Ker, 1895, *Mrs. Gribble* (MEL); Cairns, Fresh Water Creek, common, moist forest, 500 ft alt, Jan. 29, 1958, *H. St. John 26,237* (BISH).

[1] B. P. Bishop Museum, Honolulu, Hawaii. Manuscript received December 3, 1962.
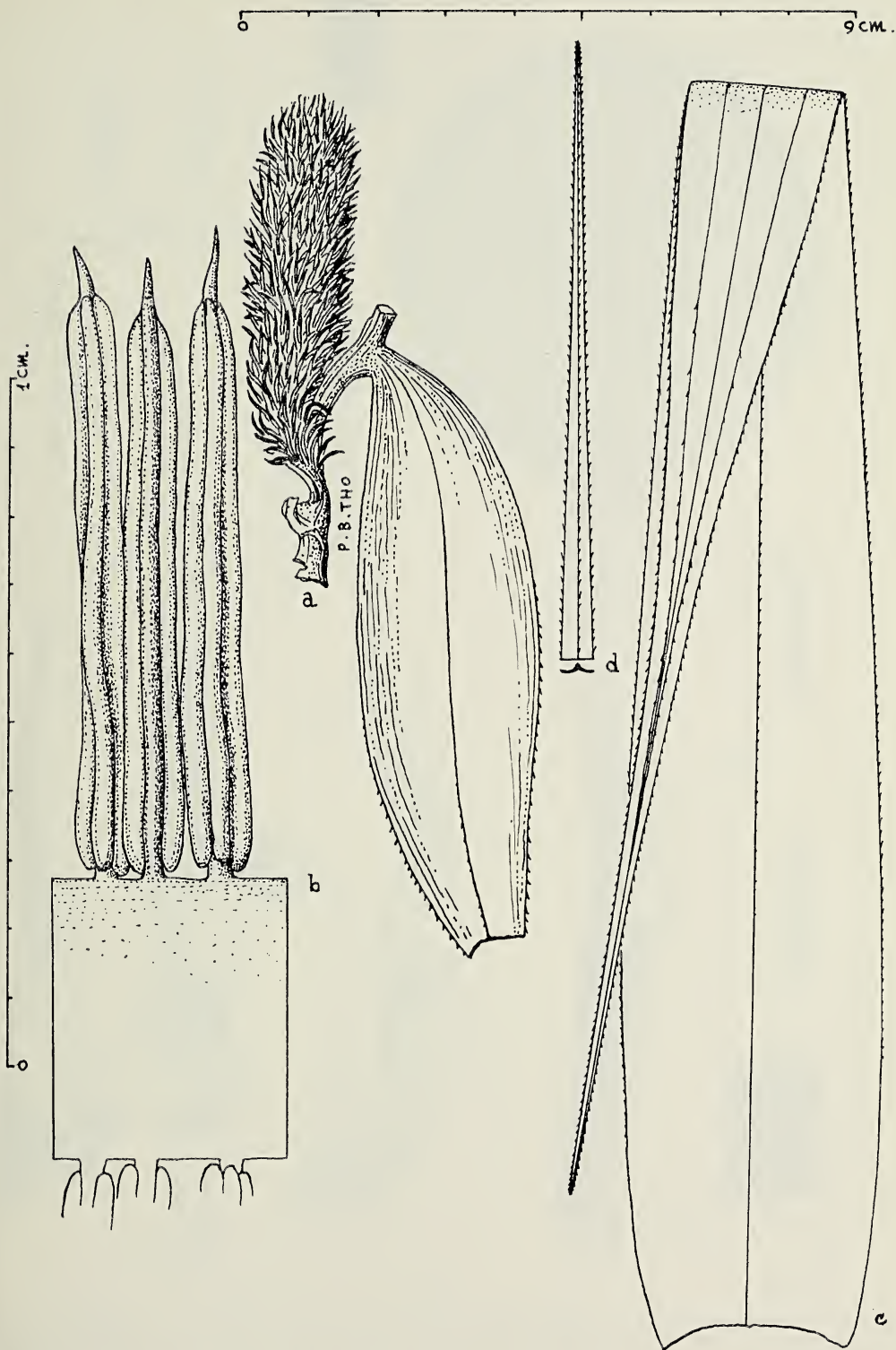
FIG. 232. *Pandanus monticola* F. Muell., from holotype. *a*, Staminate spike and bract, × 1; *b*, stamens and axis, × 10; *c*, leaf, showing upper side of apex, × 1; *d*, leaf apex, lower side, × 1.
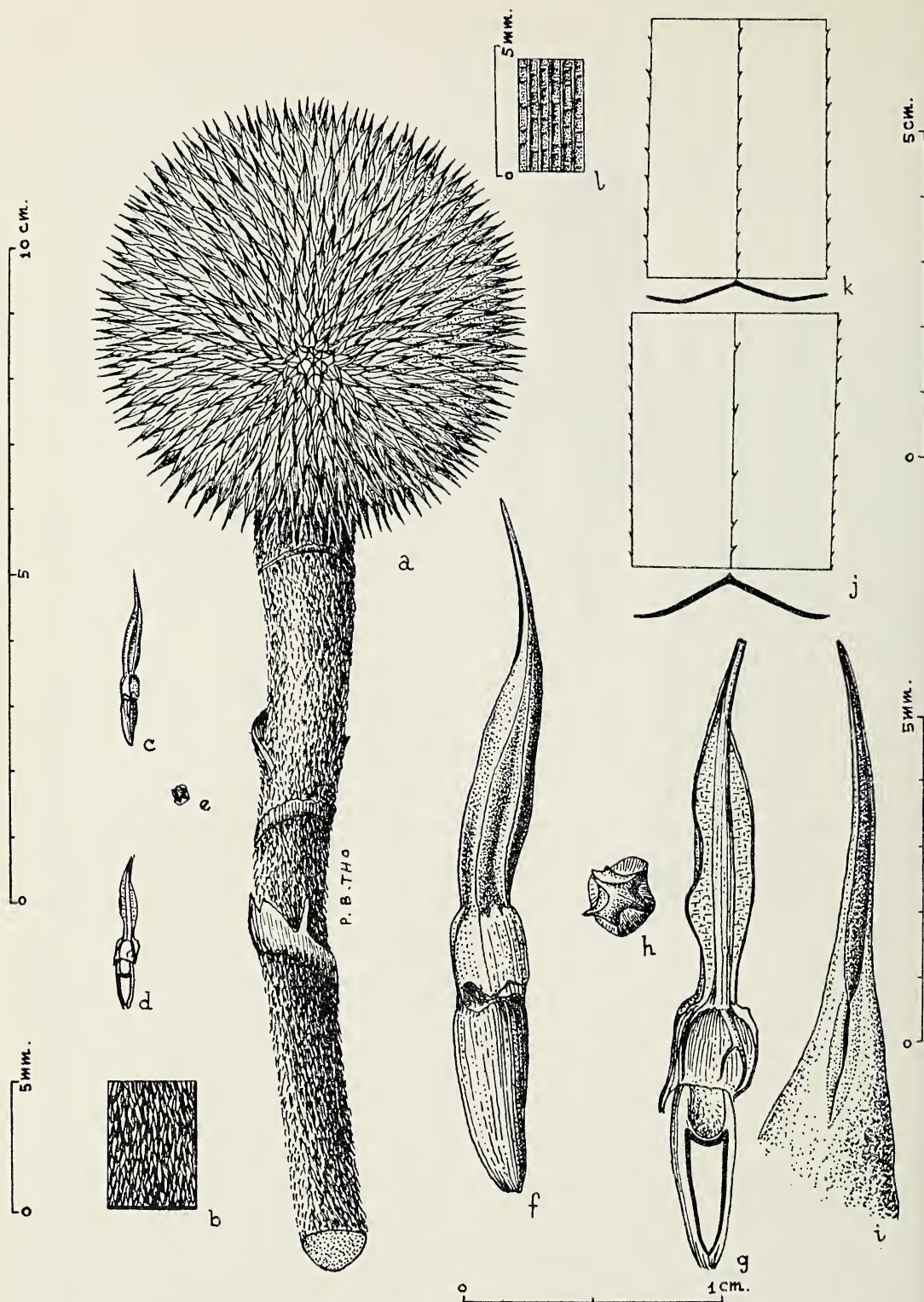
FIG. 233. *Pandanus monticola* F. Muell., from Queensland, Russell R., 1886, *F. von Mueller* (MEL). *a,* Syncarp and peduncle, × 1; *b,* part of peduncle, × 4; *c,* drupe, lateral view, × 1; *d,* drupe, longitudinal median section, × 1; *e,* drupe, apical view, × 1; *f,* drupe, lateral view, × 4; *g,* drupe, longitudinal median section, × 4; *h,* drupe, apical view, × 4; *i,* style and stigma, × 10; *j,* leaf base, lower side, × 1; *k,* leaf middle, lower side, × 1; *l,* venation of lower leaf surface, × 4.
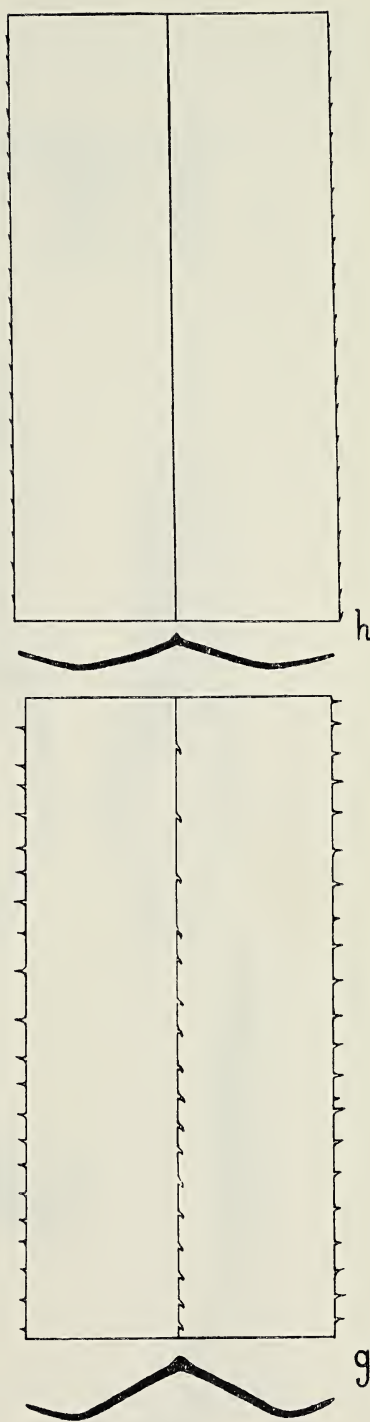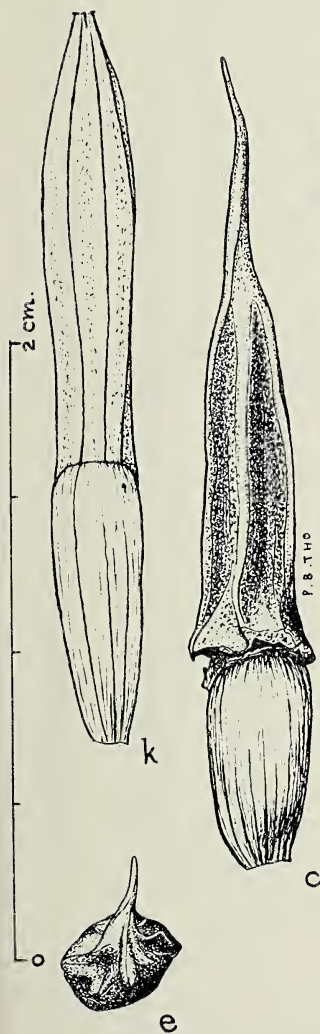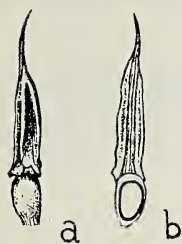
FIG. 234. *Pandanus monticola* F. Muell., *a–j* from *St. John 26,237; k,* from "valle Dalrympli," *J. Dallachy* (MEL). *a,* Drupe, lateral view, × 1; *b,* drupe, longitudinal median section, × 1; *c,* drupe, lateral view, × 4; *d,* drupe, longitudinal median section, × 4; *e,* drupe, apical view, × 4; *f,* style and stigma, × 4; *g,* leaf base, lower side, × 1; *h,* leaf middle, lower side, × 1; *i,* leaf apex, lower side, × 1; *j,* leaf apex, upper side, × 1; *k,* drupe, lateral view, × 4.

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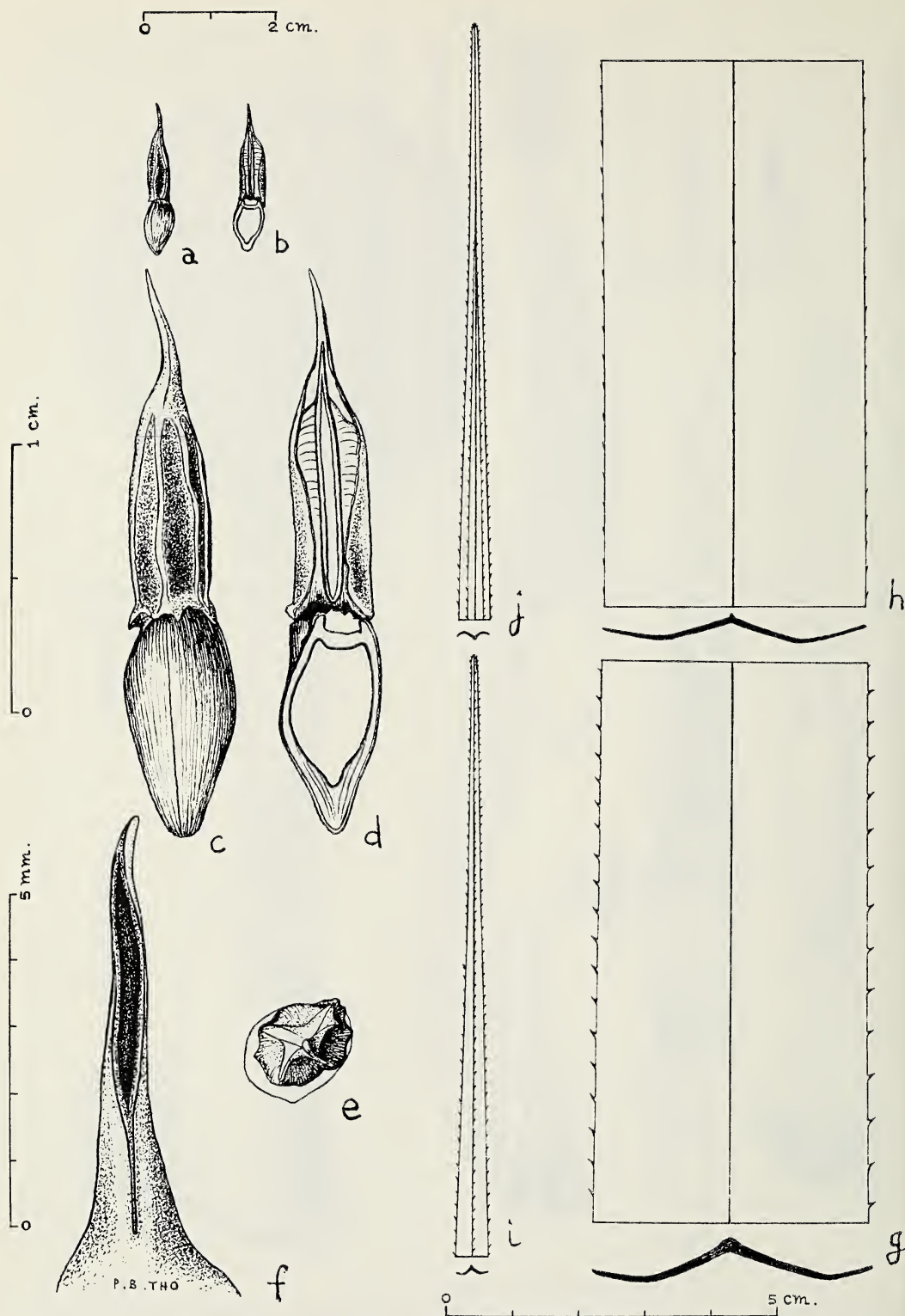
FIG. 235. *Pandanus pluvisilvaticus* St. John, from holotype. *a,* Drupe, lateral view, × 1; *b,* drupe, longitudinal median section, × 1; *c,* drupe, lateral view, × 4; *d,* drupe, longitudinal median section, × 4; *e,* drupe, apical view, × 4; *f,* style and stigma, × 10; *g,* leaf base, lower side, × 1; *h,* leaf middle, lower side, × 1; *i,* leaf apex, lower side, × 1; *j,* leaf apex, upper side, × 1.
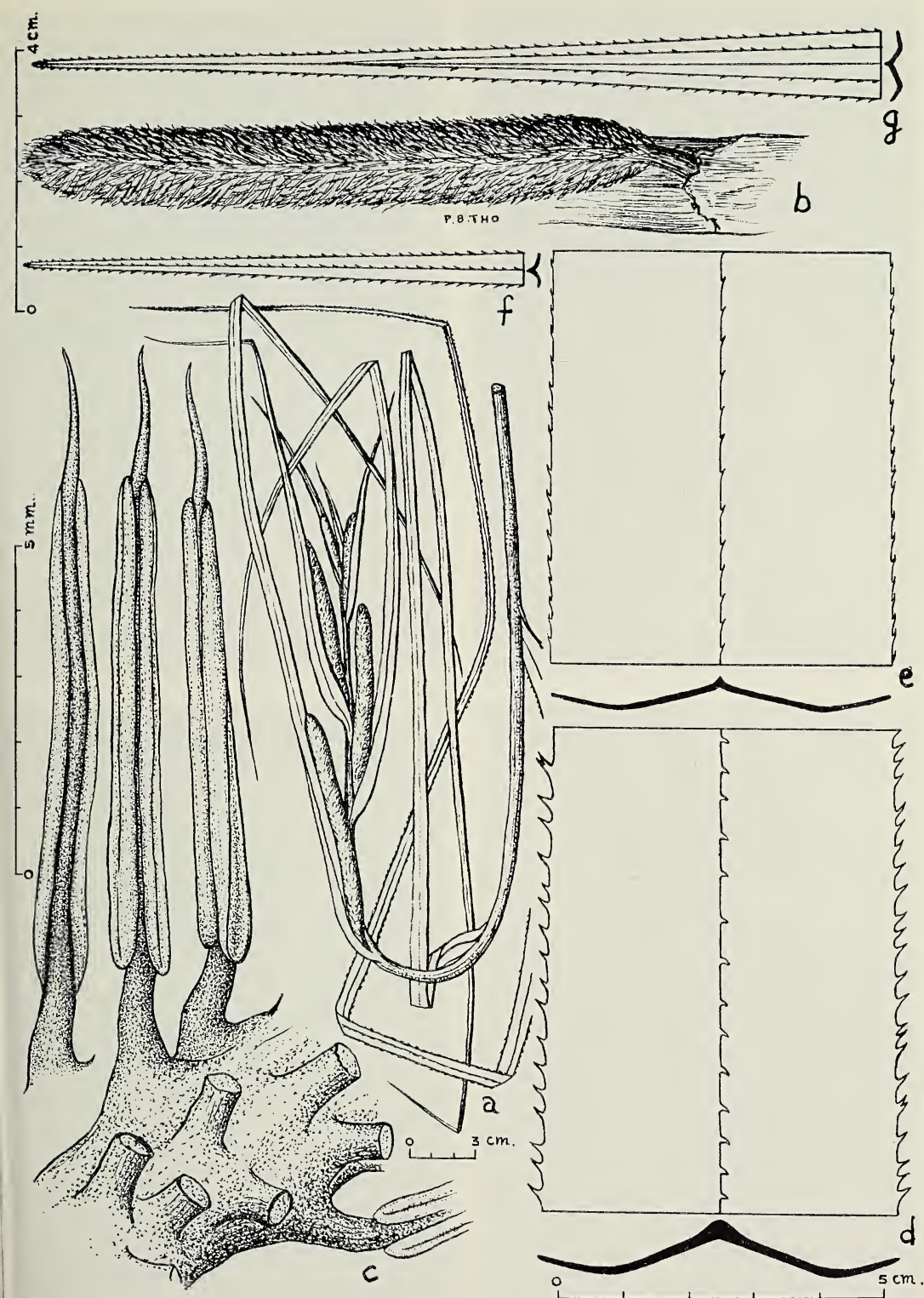
Fig. 236. *Pandanus pluvisilvaticus* St. John, from *St. John 26,254. a,* Staminate inflorescence, × 1/3; *b,* staminate spike, × 1; *c,* stamens and axis, × 10; *d,* leaf base, lower side, × 1: *e,* leaf middle, lower side, × 1; *f,* leaf apex, lower side, × 1; *g,* leaf apex, upper side, × 1.

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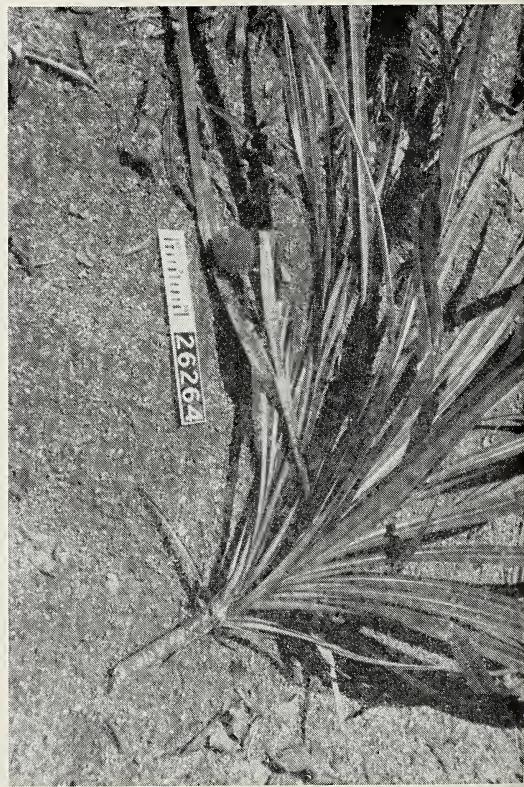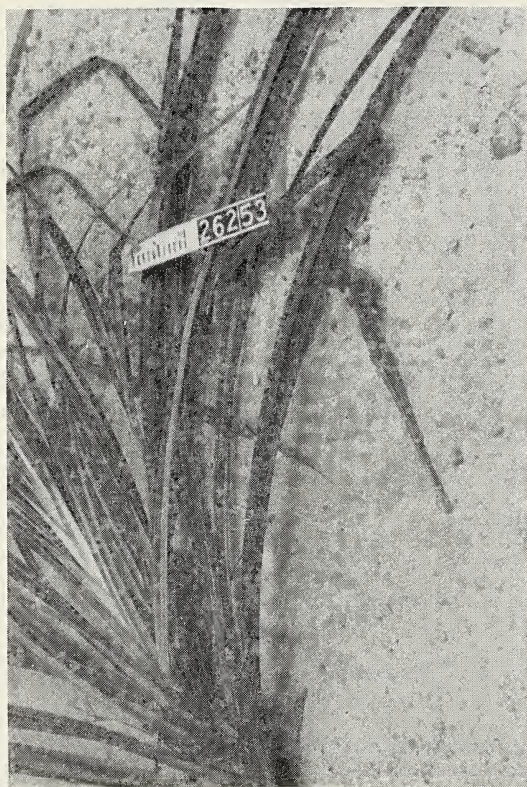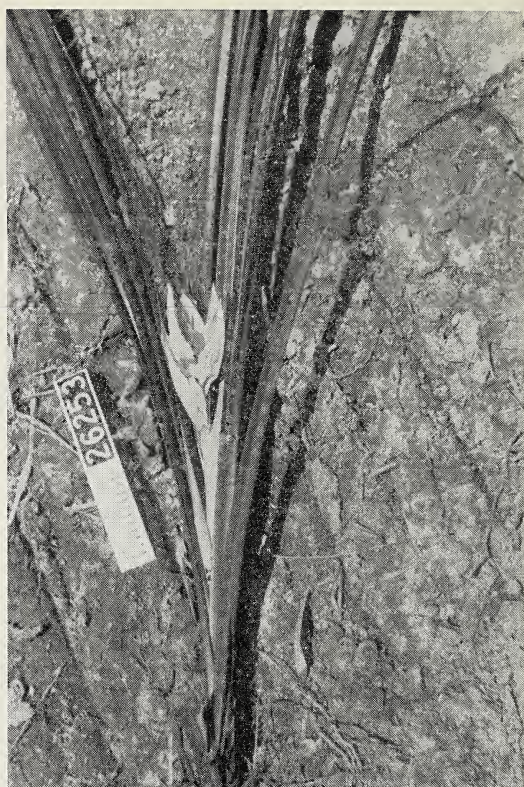
DISCUSSION: *P. monticola* F. Muell. belongs in the section *Acrostigma*. Its author, Baron von Mueller, published upon it three times. In 1865 he published the binomial for it as a doubtful species, and gave a casual reference to fruit characters. The type locality was Rockingham's Bay, but the authenticating specimen preserved in the Melbourne herbarium, collected in 1864 by J. Dallachy, consists of one leaf and parts of a staminate inflorescence. This is taken to be the holotype.

His second publication, in 1870, was based upon study of a collection from "valle Dalrympli," also by J. Dallachy. Here, von Mueller positively adopted the species and gave a good description, including characters of the scarlet fruit.

In 1874 he published on it a third time, supplementing the herbage characters, and describing the staminate flowers.

Pandanus pluvisilvaticus sp. nov. (sect. *Acrostigma*)

Figs. 235–237

DIAGNOSIS HOLOTYPI: Frutex 4 m altus, caulibus plerumque simplicibus 3 cm diametro erectis inermibus, radicibus fulturosis nullis, foliis 1.45–1.66 m longis proxima basem 4.1 cm latis in medio 3.8–3.9 cm latis ligulatis subcoriaceis supra viridibus infra pallide viridibus sensim in apice subulato diminuentibus eo in puncto 10 cm ex apice 4.5 mm lato in sectione M-formatis, basi inermi amplexicauli sed ex 2.5–3 cm marginibus cum aculeis 1.5–2 mm longis 2–5 mm separatis subulatis adscendentibus stramineis, midnervo proximali inermi, in sectione mediali marginibus cum aculeis 0.5–1 mm longis 3–7 mm separatis subulatis adpresse adscendentibus, midnervo infra proximali cum aculeis 0.3–0.5 mm longis 5–10 mm separatis subulatis adscendentibus, proxima apicem marginibus et midnervo infra subulatoserratis dentibus 0.4–0.6 mm longis eis marginalium 1–2 mm separatis illis midnervi 2–5 mm separatis, supra plicis lateralibus cum serrulis 0.5–0.8 mm longis 2–5 mm separatis, inflorescentia foeminea terminali, pedunculo 44

cm longo 7–8 mm diametro acute trigono cum bracteis foliosis paucis superiore 39 cm longa 2 cm lata, syncarpio ex 6–7 bracteis albis subpetaloideis sustento, eis medialibus superisque 7–10 cm longis 3 cm latis lanceolatis minute aciculari-ciliatis, syncarpio 6 cm longo 5.5 cm diametro latiter obovoideo solitario terminali erecto cum drupis multis adpressis, drupis 20–22 mm longis 4 mm latis 3 mm crassis rubris pilei 6.5–12 mm longo 5–6-anguloso libero corpore laevi ellipsoideo sed argute anguloso, parte ⅗ supera libera, stylo 3.5–4.5 mm longo subulato subcurvato plerumque distaliter curvato, stigmate 3–4 mm longo lineari distali brunneo papilloso, endocarpio in parte ¼ infera 7 mm longo cartilagineo luteo lateribus 0.2 mm crassis in apice in lateribus cavernae extento, semine 5 mm longo 3–4 mm diametro latiter ellipsoideo sed in apice concavo, mesocarpio apicali in centro cum fibris fortibus et cum lateribus carnosis, mesocarpio basali sparso fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Shrub 4 m tall; stems mostly simple, pale brown, 3 cm in diameter, erect, unarmed; prop roots none; leaves 1.45–2.33 m long, 3.8–5.4 cm wide near the base, 3.3–5.1 cm wide at the middle, ligulate, subcoriaceous, green above, pale green below, gradually tapering to the subulate apex, this 10 cm down 4.5 mm wide, in section M-shaped, the base unarmed, amplexicaul but beginning at 2.5–3 cm up the margins with prickles 1.5–2 mm long, 1–5 mm apart, subulate, ascending, stramineous, the nearby midrib unarmed, or with reflexed prickles 1–1.5 mm long, 2–5 mm apart; at midsection the margins with prickles 0.5–1 mm long, 3–7 mm apart, subulate, appressed ascending; the nearby midrib below with prickles 0.3–1 mm long, 3–10 mm apart, subulate, ascending; near the tip the margins and midrib below subulate-serrulate, the teeth 0.4–0.6 mm long, those of the margins 1–2 mm apart but those of the midrib 2–5 mm apart; above the lateral pleats with ascending serrulations 0.5–0.8 mm long, 2–5 mm apart; pistillate inflores-

FIG. 237. *Pandanus pluvisilvaticus* St. John. *a–c,* From holotype: *a (upper left),* habit, and figure of Dr. S. T. Blake of Brisbane; *b (upper right),* inflorescence in anthesis, showing the white bracts; *c (lower left),* leafy branch with mature syncarp; *d (lower right),* from *St. John 26,264,* leafy branch with mature syncarp.

cence terminal; peduncle 35–65 cm long, 7–8 mm in diameter, sharply trigonous, with a few leafy bracts, the uppermost one 39 cm long, 2 cm wide; syncarp subtended by 6–7 pure white, subpetaloid bracts, the middle and upper ones 7–10 cm long, 3 cm wide, lanceolate, finely acicular ciliate; syncarp 6–11 cm long, 5.5–7 cm in diameter, broadly obovoid, single, terminal, erect, bearing numerous, crowded drupes, these 20–28 mm long, 4 mm in diameter, 3 mm thick, red to orange; pileus 5–6-angled, upper ½–⅗ of drupe free, pileus 6.5–12 mm long, the surface smooth, the body ellipsoid but with sharp ridges and deep rounded valleys; style 3.5–4.5 mm long, subulate, slightly curved, usually away from apex of syncarp; stigma 3–4 mm long, distal, linear, brown, papillose; endocarp in lower ¼, and 7–11 mm long, cartilaginous, yellowish, the walls 0.2 mm thick, and at its summit enclosing all but the top of a fat discoid cavity; seed 5–6 mm long, 3–5 mm in diameter, broad ellipsoid except for the concave apex; apical mesocarp with strong central fibers and soft pith forming the side tissues; basal mesocarp sparse and this fibrous and fleshy.

Staminate plants 10 m tall, 20 mm in diameter; prop roots none; leaves 2.4 m long, 5 cm wide near the base but at the middle 5.2 cm wide, the base amplexicaul, entire, beginning 5–6 cm up the margins with spines 2–3 mm long, 1–6 mm apart, stout serrae with subulate tips, single or a few doubled or trebled, yellowish; the midrib below beginning at 12.5 cm up with stout retrorse serrae, 1–1.5 mm long, 2–8 mm apart; at the midsection the margins with teeth 1–1.5 mm long, 3–6 mm apart, subulate, appressed ascending; the midrib below sharp, raised, with similar teeth, but heavier based; near the apex the margins and the midrib below and the two secondary pleats above with serrae 0.8–1 mm long, 1–2 mm apart; the blade gradually narrowed to the subulate trigonous apex, the very tip lost, but about 10 cm down the tip 10 mm wide; staminate inflorescence 65 cm long, sparsely leafy bracted, the middle bract of the peduncle 110 cm long, 6 cm wide, foliaceous, the midrib below and the margins spiny to serrate, the apex subulate, the peduncle 40 cm long, the main raceme with 8–10 lateral racemes, each

subtended by a white, semipetaloid bract, the lower ones 40 cm long, 3 cm wide, the apical half green and foliaceous; lateral racemes 6–10 cm long, including the 5–7-mm stipe, 15 mm in diameter, densely flowered; stamens distinct; free filament 0.7–1.6 mm long; anthers 6–7 mm long, linear, yellow, bearing an apical prolongation of the connective 1–2 mm long, subulate.

HOLOTYPUS: Australia, North Queensland, Kuranda, Black Mt. Road, rain forest with *Acacia, Calamus,* and *Gahnia,* 1,000 ft alt, Feb. 4, 1958, *H. St. John 26,253* (BISH).

SPECIMENS EXAMINED: Australia, North Queensland, 11 miles N. of Mossman, rain forest with *Calamus, Myristica,* and *Hibiscus tiliaceus,* 20 ft alt, Feb. 6, 1958, *St. John 26,264* (BISH); 5 miles N. of Gadgarra Forest Station, 5 miles E. of Yungabarra, rain forest, 2,130 ft alt, Feb. 11, 1958, *St. John 26,277* (drupes sterile) (BISH); Bloomfield R., 1883, *Barnard* (MEL); Russell R., 1886, *F. von Mueller* (MEL); near Mulgrave R., [*F. von Mueller*] 144 (MEL); Daintree R., 1882, *Pentzke* (MEL); 11 miles N. of Mossman, rain forest with *Calamus, Myristica, Hibiscus tiliaceus,* 20 ft alt, Feb. 5, 1958, *St. John 26,263* (BISH).

DISCUSSION: *P. pluvisilvaticus* is a member of the section *Acrostigma,* as is its closest relative *P. monticola* F. Muell., a species with the endocarp 4–6 mm long, and with the seed forming ¼–⅓ of the drupe; pileus 13–14 mm long; stigma 5–6 mm long; anthers oblong-linear; free filament tips 0.1–0.2 mm long; and the leaves 32–43 mm wide. *P. pluvisilvaticus* has the endocarp 7–11 mm long, and with the seed forming ⅖–½ of the drupe; pileus 6.5–12 mm long; stigma 3–4 mm long; anthers tapering upward; free filament tips 0.7–1.3 mm long; and the leaves 36–58 mm wide.

P. pluvisilvaticus is actually a common species, but it has been confused with the rather poorly described *P. monticola* F. Muell., which occurs in eastern Queensland in the rain forests at from 18° to 21° South. It has been reported by von Mueller from the Russell River at 17° 30′ South, but he also had a col-

lection of *P. monticola* with exactly duplicating data. There may have been a confusion in the data of these two collections.

P. pluvisilvaticus occurs in the rain forests of eastern Queensland from 17° to 16° South, and is known from numerous collections. It shows some variability in the width of the leaf blades and considerable variation in the leaf spines, but it seems to represent a taxon of fairly wide distribution. Its fruit characters are dependable as a basis for separation from the older *P. monticola* F. Muell.

The new epithet is coined from the Latin *pluvia,* rain, and *silvaticus,* woodsy, and is given with reference to the habitat of the species, the rain forest.

Revision of the Genus *Pandanus* Stickman, Part 22
A New Species (Section *Hombronia*) from New Caledonia

HAROLD ST. JOHN[1]

NUMEROUS BOTANISTS in the tropics of the Pacific and of the eastern hemisphere have assisted the writer by making new collections of *Pandanus*. The new species here announced is named in honor of one of these coöperators, Prof. H. S. McKee of the University of Sydney.

Pandanus Mc-Keei sp. nov. (sect. *Hombronia*)
Figs. 238–239

DIAGNOSIS HOLOTYPI: Arbor 5 m alta ramosa, radicibus fulturosis nullis, foliis 1.5 m longis proxima basem 7.2 cm latis in medio 6.5 cm latis coriaceis supra obscure viridibus infra pallide viridibus basi rubra ligulatis gradatim ex media ad apicem diminuentibus, basi paene latiore exarmata sed ex 11–12 cm marginibus cum aciculato-serris 1–1.5 mm longis 1–5 mm distantibus eis in puncto nigro, midnervo toto exarmato, circa medim marginibus cum serris nigris 0.3–0.5 mm longis 2–6 mm distantibus, circa apicem marginibus cum dentibus nigris crenulatis 0.1–0.3 mm longis 1–3 mm distantibus; pedunculo folioso, syncarpio solitario apicali 36 cm longo 17 cm diametro anguste oblongo-ellipsoideo cum circa 286 phalangibus ordinatis in helicis et sereis verticalibus, phalangibus 4.2–4.6 cm longis 2.4–3.1 cm latis 1.5–2 cm crassis rubro-brunneis sed intra pallide luteis elliptico-oblongis in medio subcontractis parte supera ¼ libera apice concavo in sicco brunneis, lateribus minime curvatis et cum fissuris multis brunneis longitudinalibus, 5–6-angulosis, suturis lateralibus nullis, carpellis 5–7 in plano unico laterali ordinato, stigmatibus 1.5–2.6 mm latis brunneis cordatis vel obliquiter cordatis in latere ad apicem syncarpii obtutis, endocarpio in parte ¼ infera et 12–14 mm longo osseoso brunneo lateribus 3–4 mm crassis, seminibus 6–8 mm longis 2–3 mm diametro ellipsoideo, mesocarpio caverno unico 25 mm longo pluri-fibroso et cum membranis albis medullosis formanti, mesocarpio basali fibroso et cavernoso 3–6 mm longo.

DESCRIPTION OF HOLOTYPE: Tree 5 m tall, branched several times; prop roots none; leaves 1.5 m long, 7.2 cm wide near the base, 6.5 cm wide at the middle, coriaceous, dark-green above, light-green below, base red, ligulate, gradually tapering from the middle to the apex, the base scarcely widened, unarmed, beginning at 11–12 cm the margins acicular-serrate, the teeth 1–1.5 mm long, 1–5 mm apart, black-tipped; the midrib unarmed throughout; at the midsection the margins black serrulate, the teeth 0.3–0.5 mm long, 2–6 mm apart; near the apex the margins black crenulate, the teeth 0.1–0.3 mm long; peduncle leafy bracted; syncarp solitary, terminal, 36 cm long, 17 cm in diameter, narrowly oblong-ellipsoid, the phalanges about 286, in spiral and in vertical rows; phalanges 4.2–4.6 cm long, 2.4–3.1 cm wide, 1.5–2 cm thick, reddish-brown without, light-yellow within, elliptic-oblong, slightly contracted at midsection, upper ¼ free; apex concave, dull, brownish when dry, the exposed sides gently curving and with numerous longitudinal, brown cracks, 5–6-angled; lateral sutures none; carpels 5–7, in one lateral plane; stigmas 1.5–2.6 mm wide, brown, cordate or obliquely so, facing sideways toward the apex of the syncarp; endocarp at lower ¼ and 12–14 mm long, bony, brown, the lateral walls 3–4 mm thick; seeds 6–8 mm long 2–3 mm in diameter, ellipsoid; apical mesocarp forming one cavern 25 mm long, with an open passage above each seed, with numerous, strong, longitudinal fibers and pale medullary membranes; basal mesocarp fibrous and cavernous, 3–6 mm. long.

HOLOTYPUS: New Caledonia, 7 km. S. of Rivière des Pirogues, on bank of creek, 50 m alt, 15 Oct., 1955, *H. S. McKee 3,229* (BISH). Isotype(L)!

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[1] B. P. Bishop Museum, Honolulu, Hawaii. Manuscript received December 3, 1962.
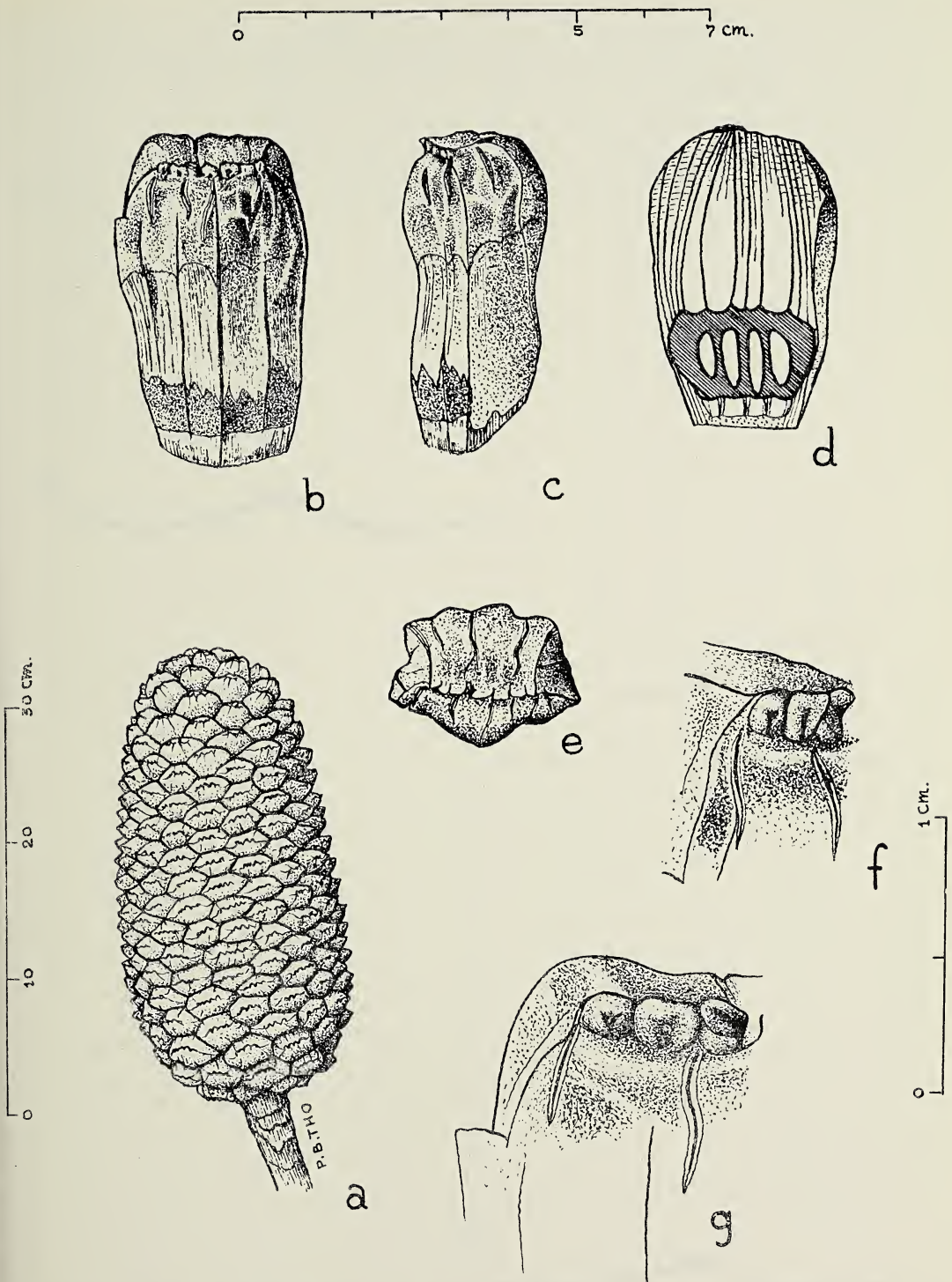
FIG. 238. *Pandanus Mc-Keei* St. John, from holotype. *a,* Syncarp, lateral view, × 1/5; *b,* drupe, proximal view, × 1; *c,* drupe, lateral view, × 1; *d,* drupe, longitudinal median section, × 1; *e,* drupe, apical view, × 1; *f, g,* stigmas, proximal view, × 4.
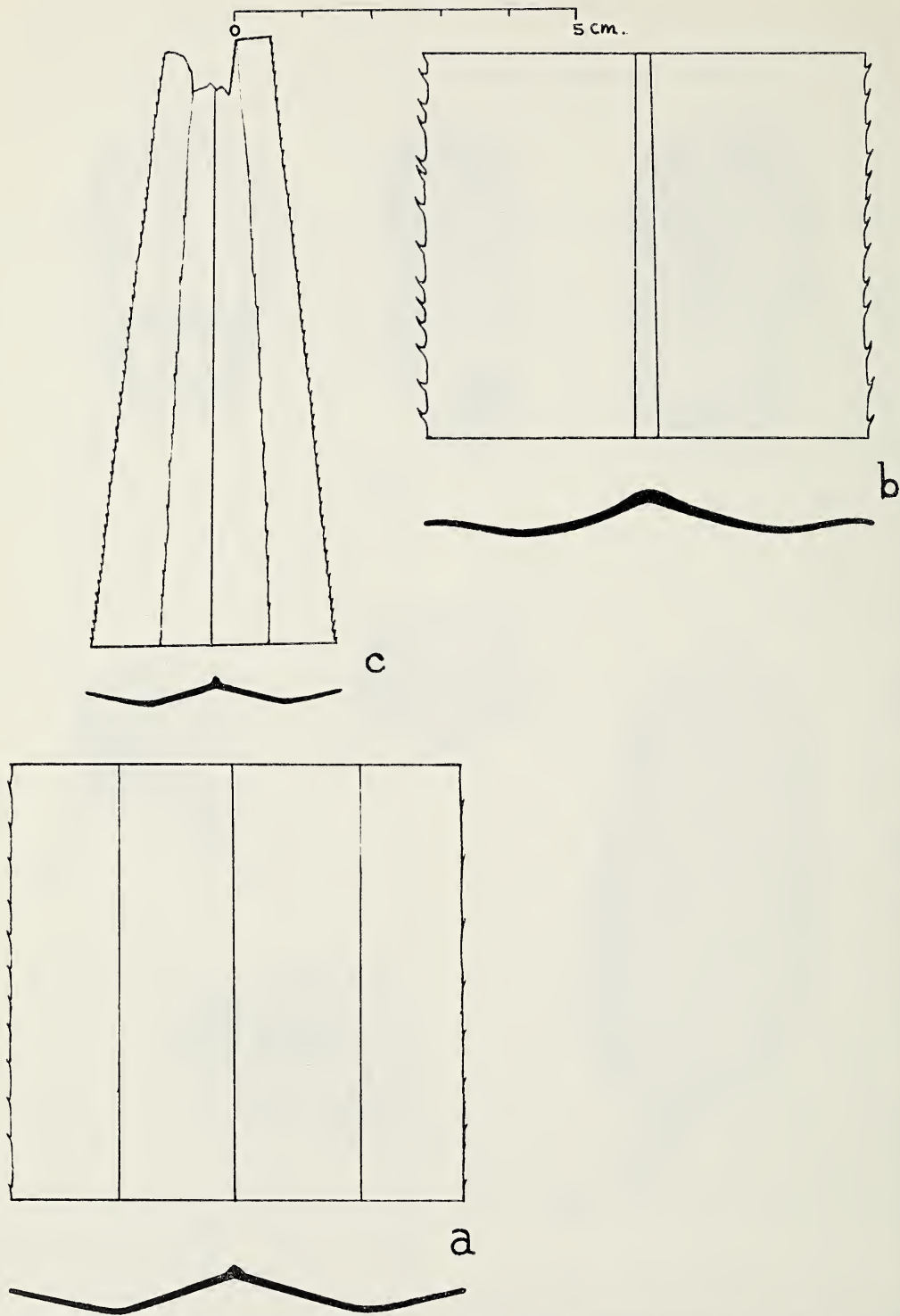
FIG. 239. *Pandanus Mc-Keei* St. John, from holotype. *a,* Leaf middle, lower side, × 1; *b,* leaf base, lower side, × 1; *c,* leaf apex, upper side, × 1.

DISCUSSION: *P. Mc-Keei* is a member of the section *Hombronia*. There its closest relative is *P. Balansae* (Brongn.) Solms of New Caledonia, which species has the syncarp 17–18 cm long, 13–14 cm in diameter; phalanges 5.5 cm long, 2.5 cm wide, the apex pyramidal to truncate apex which is half as wide as the phalange; carpels 3–6; and endocarp at the lower third of the phalange. *P. Mc-Keei* has the syncarp 28.8 cm long, 12.8 cm in diameter; phalanges 4.2–4.6 cm long, 2.4–3.1 cm wide, the convex apex nearly as wide as the body; carpels 5–7; and the endocarp at the lower ¼ of the phalange. The species is dedicated to Prof. H. S. McKee, the collector.

Soil-Vegetation Relationships in Hawaiian Kipukas[1]

D. Mueller-Dombois and C. H. Lamoureux[2]

KIPUKA, the Hawaiian word for "opening," has come into scientific usage as a term used to designate an older area on the slopes of volcanic mountains that has been surrounded by more recent lava flows. Kipukas are common landscape features on the slopes of Mauna Loa and Kilauea volcanoes on the island of Hawaii, where they can be readily recognized as islands of denser vegetation in the vast, sparsely vegetated areas. They range in size from a few square meters to hundreds of acres.

Kipukas are of special interest for several reasons. As vegetation islands they provide seed-source centers for the invasion of vegetation on new volcanic material. As vegetation islands they represent somewhat simplified ecosystems, analogous to bogs or lakes, that are very suitable for studying internal ecological relationships. The isolation of small populations in kipukas provides unique opportunities for evolutionary studies.

So far, very little ecological work has been done with Hawaiian kipukas. Need for such work has arisen in Hawaii Volcanoes National Park, where the Park Service is confronted with the task of interpreting certain kipuka features to the Park visitors. Kipuka Puaulu, popularly known as "Bird Park," has been accessible to the public for some time and the nearby Kipuka Ki is soon to be opened. For this reason the present study was begun in these two kipukas.

Rock described the flora of both kipukas in an undated manuscript (probably written around 1910) and reported a few general ecological observations. He remarked upon the unique and complex composition of arborescent species from which he judged both kipukas to be "of great age." However, as an approximation he cited the estimate of Professor T. Jaggar (geologist at the Hawaii Volcano Observatory at that time), which placed the kipuka's origin within the Christian era (i.e., less than 2,000 years). Rock recorded 40 arborescent native species forming a complex forest type in Kipuka Puaulu. Only half this number of tree species were found in Kipuka Ki. He also noted the presence of two vegetation types in Kipuka Puaulu, a complex forest type containing many tree species and a *Metrosideros*-dominated type. He believed that soil differences were responsible for the presence of these two types of forest. A general description of the kipuka soils is given in the Soil Survey report for the Territory of Hawaii (Cline et al., 1955), where the soils were classified as Latosolic Brown Forest soils derived from two layers of volcanic ash.

The primary objectives of this present study were to determine the floras of both kipukas, to describe the vegetation types present in each, and to determine what soil-vegetation relationships exist in these places.

DESCRIPTION OF AREA

Both kipukas occur at an elevation of from 1200 to 1300 m on the southeast slope of Mauna Loa approximately 3 km northwest of Kilauea crater (Fig. 1). The central elevation of Kipuka Ki is about 60 m higher than that of Kipuka Puaulu. Both are surrounded and separated by recent beds of rough aa lava. Their boundaries are about 800 m apart. Kipuka Puaulu is about 42 hectares and Kipuka Ki about 18 hectares in size. The climate is characterized by a rather uniform mean annual temperature of 16°C, which is 7°C cooler than that experienced at sea level. The mean variation between the warmest month (August) and the coolest (February) is only 3.5°C. Occasional freezing temperatures can be expected during February nights. Approximate annual rainfall is 1500 mm, varying monthly from about 25 mm in June to 200 mm in January. According to Krajina's (1963) zonal classification, the ki-

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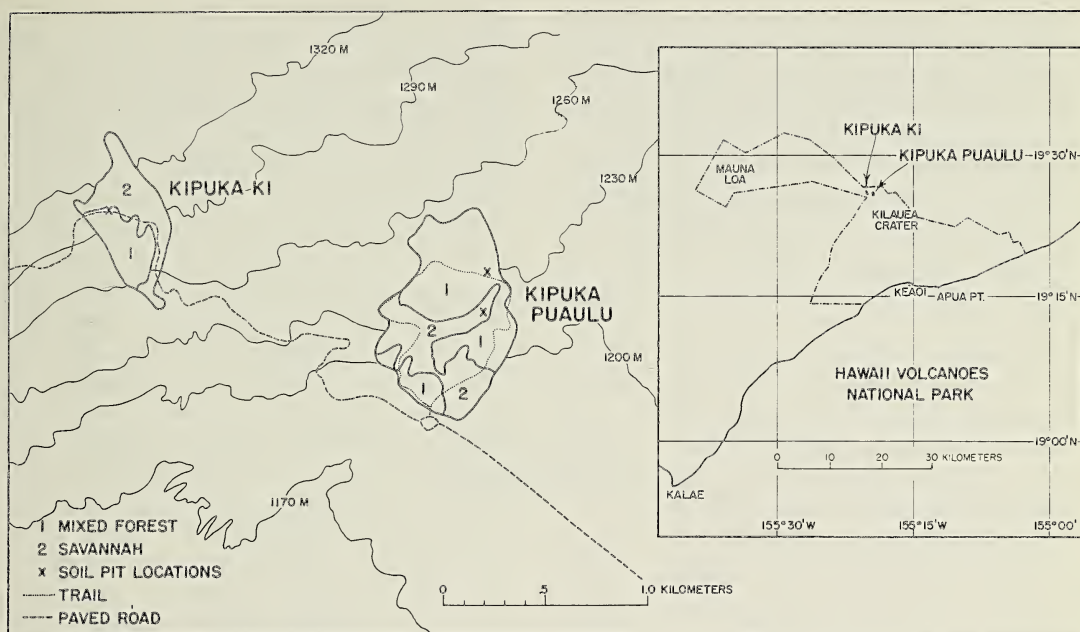
FIG. 1.   Map of kipukas showing major vegetation types and soil pit locations. (Drawn from 1:12,000 air photo taken October 1954.)

pukas occur in the lower *Metrosideros* zone, whose climate is described as humid marine tropical (or subtropical) with common clouding. The kipukas are somewhat more sheltered from the windward rains than much of this zone, and Rock (1913) described them as being occupied by dry-mixed forest.

Both kipukas are situated on moderate south slopes and have an irregularly undulating topography with a few short, steep slopes, several level areas, a few larger somewhat inclined areas, and scattered small pocket-like depressions.

Two distinct vegetation formations were found in Kipuka Puaulu: a closed to semi-open forest type (Fig. 1, type 1), and a savannah type with a dense grass cover and scattered trees of *Metrosideros* and *Acacia koa* (Fig. 1, type 2). Kipuka Ki is dominated by a moderately stocked forest vegetation type, which in places is also semi-open (Fig. 1, type 1), but it lacks the very dense or closed forest stand segments found in Kipuka Puaulu: a closed to semi-open also in Kipuka Ki, representing there, however, mainly a transition zone in which occasional lava rocks protrude to the surface (Fig. 1,

type 2). Characteristically, no rocks are found near the surface in either kipuka with the exception of the transitory savannah in Kipuka Ki. Within the forest formation of both kipukas several smaller plant communities can be recognized. One of the more obvious associations, common to both kipukas, is characterized by a ground cover of *Microlepia setosa*, a lush fern up to 1 m tall. The tree layer is dominated by *Acacia koa* and *Sapindus saponaria*. This plant association occurs on level to moderately sloping ground.

METHODS

For the purpose of comparing the soils of the two kipukas, soil pits were dug in each kipuka in the *Microlepia* community near a tall *Acacia koa* tree in a level place. A level place near a tall koa tree was also chosen for a soil pit in the savannah for making a comparison between the soils of the forest and the savannah formation within Kipuka Puaulu (Fig. 1). The reason for choosing a level place was that the soils there were presumably not influenced by lateral seepage.

Each pit was dug to a depth of 2 m. The soil horizons were described as to depth, material, and color, and samples were collected for laboratory analysis. The soil samples included three sets, one for microbiological analyses (now being conducted), one for current soil moisture analysis, and one for other soil tests. In addition, the three soil profiles were prepared as soil monoliths after the method of Smith and Moodie (1947) for further mega- and microscopic inspection and as permanent records.

Subsequent soil tests carried out included determination of moisture equivalents (by the centrifuge method), permanent wilting percentages (by the sunflower method), organic carbon (by the Walkley-Black wet-combustion method), and pH (by electric pH meter).

Herbarium specimens were prepared. One set has been deposited in the herbarium of the University of Hawaii, and a second set in the herbarium of Hawaii Volcanoes National Park.

RESULTS AND DISCUSSION

A. Soils

The soils give convincing evidence that they have been derived from volcanic ash and not from old, disintegrated lava as has been assumed by the authors who published the nature trail guide for Kipuka Puaulu (1961 edition). Ash strata were found to the depth of 2 m to which all soil pits were dug and there was no sign of parent material change at this depth. Rock (undated) indicated that the soil in Kipuka Puaulu was nearly 6 m deep. The maximum soil depth in Kipuka Ki is not known.

Ash was deposited not at one time but in several stages, probably extending over many hundreds of years. Corresponding ash layers that appear to have originated from the same eruptions can be found in all soils we examined. Noteworthy are two thin red pumice layers that occur in each soil. One occurs in the lower profile at 100 cm depth in the soil of Kipuka Ki, at 140 cm in the forest soil of Kipuka Puaulu, and at 145 cm in the savannah soil (Fig. 2). A second red pumice layer is found in all soils nearer the surface, at 60 cm in Kipuka Ki, at 70 cm in the forest soil of Kipuka Puaulu, and at 85 cm in the savannah soil.

Ash deposits were composed of at least five different materials: a fine, dusty gray ash with scattered pebbles up to 5 mm in diameter, a gravelly ash with basaltic and variously vesicular pebbles up to 1 cm in diameter, a black vitreous ash, a yellow-olive pumice, and the red pumice mentioned above.

The fine, dusty gray ash occurs at a depth of 15–20 cm from the surface in all profiles. It is most pronounced in the savannah soil and least so in the soil of Kipuka Ki. This layer looks like the leached layer of a podzolic soil. However, there are three arguments against this interpretation. First, the layer is brightest under savannah, which has the least acid surface layer (Table 1). Second, it was horizontally continuous only in Kipuka Puaulu, whereas it occurred in local pockets in Kipuka Ki. Third, Wentworth (1938), in his study of ash formations around Kilauea Crater, described a "gray-lavender, fine sand-size ash" near the surface in several places which seems to fit this layer.

The gravelly ash was described by Wentworth as "basalt in glass" and is well shown in the savannah soil, where it recurs as a thin layer (usually ± 5 cm thick) at depths of 30, 50, and 70 cm.

Black vitreous ash appears as a layer 20 cm deep in all three soils, from 50–70 cm depth in Kipuka Ki, from 60–80 cm in the forest soil of Kipuka Puaulu, and from 75–95 cm in the savannah soil. It recurs at three places above this layer (at 65 cm, 45 cm, and 25 cm) in the savannah soil. These black layers are black not only from ash but also, perhaps more dominantly so, from an extremely high incorporation of organic carbon (between 10.1 and 15.7%, Table 1).

A yellow-olive pumice layer (called "reticulite" by Wentworth) is found in the savannah soil incorporated into the black layer at 25 cm depth. Some of this pumice occurs also in both forest soils beneath the fine gray ash layer (C1), but here it is less abundant and less well stratified (Fig. 2).

The lower ash deposits, from the thick black layer (A1b) down, in both soils of Kipuka Puaulu are not stratified horizontally, whereas the upper ones are more or less horizontally stratified (see Fig. 2, P_1 and P_2). Angles of

departure were between 20 and 30°. This fact indicates that there have been some relief changes throughout the build-up of the soil to its present surface level. This suggests something about the origin of Kipuka Puaulu, which may apply to Kipuka Ki as well. It appears probable that lateral translocation of ash has occurred after deposition as a result of wind or water erosion, especially during the early stages when the kipuka was only sparsely vegetated.

A small kipuka of about 1 hectare in the Kau Desert south of Kilauea crater, which is just "in-the-making," shows that it has originated as a small dune ecosystem. Gray-black sandy ash was deposited here in a thin layer on a large flat area of smooth pahoehoe lava. Wind has swept
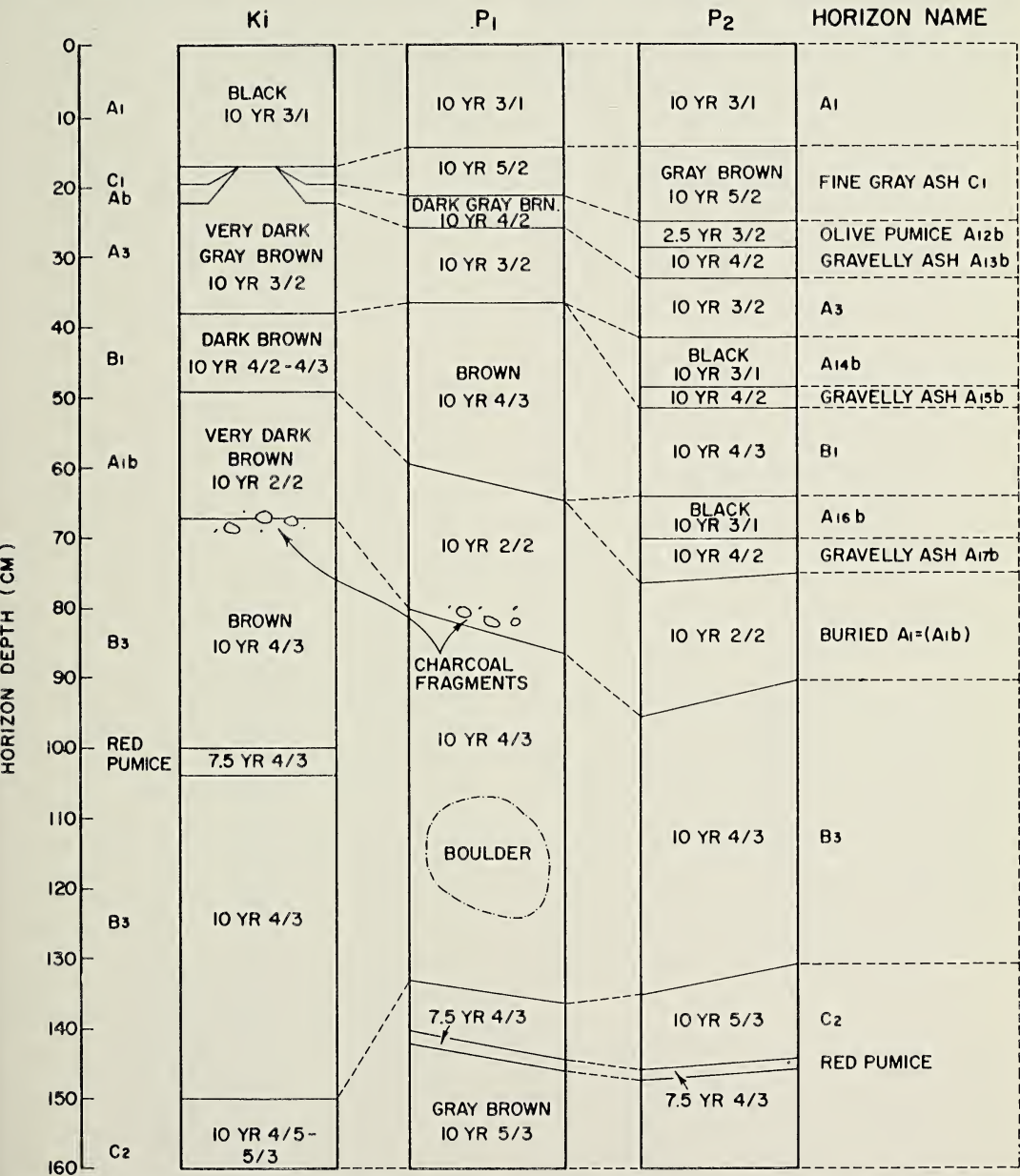
Fig. 2. Comparison of horizons of kipuka soils (*Ki*, forest soil of Kipuka Ki; *P₁*, forest soil of Kipuka Puaulu; *P₂*, savannah soil of Kipuka Puaulu). Color symbols from Munsell charts refer to air-dry soil. Nomenclature of horizons after the 1962 Supplement to the Agriculture Handbook No. 18, Soil Survey Manual.

TABLE 1

SOME PARAMETERS OF THE KIPUKA SOILS

HORIZON	CURRENT MOISTURE CONTENT (%)[1]			AVAILABLE WATER (%)[2]			ORGANIC CARBON (%)[3]			pH[4]		
	Ki[5]	P_1[6]	P_2[7]	Ki	P_1	P_2	Ki	P_1	P_2	Ki	P_1	P_2
A1	67	56	106	23	23	30	11.1	10.4	14.3	5.2	4.8	5.7
Fine gray ash C1	21	27	30	13	13	10	4.2	3.3	1.1	5.7	5.5	5.4
Olive pumice A12b	23	16	55	–	–	34	9.6	12.6	15.7	5.9	5.8	6.4
Gravelly ash A13b			17			7			15.4			5.9
A3	24	44	28	18	13	10	9.9	10.5	7.2	6.2	5.6	5.9
A14b			58			–			12.0			6.4
gravelly ash A15b			19			5			3.0			6.5
B1	29	44	44	15	16	15	7.7	7.8	5.7	5.9	5.6	5.7
A16b			48			–			13.5			6.1
gravelly ash A17b			10			3			7.8			6.3
Buried A1 (= A1b)	40	75	60	23	20	20	12.7	12.1	10.1	5.7	5.7	5.7
B3	47	42	37	9	10	5	9.0	6.9	5.4	6.0	5.7	5.9
Red pumice	53	31	16	–	–	–	3.8	3.6	1.8	5.8	5.7	7.0
C2	90	36	21	11	12	5	9.0	7.6	1.9	6.0	5.7	6.0

[1] Moisture content at date of sampling, November 23, 1963.
[2] Available water = moisture equivalent (%) – permanent wilting percentage.
[3] Walkley-Black values.
[4] Measured electrometrically.
[5] Ki = Kipuka Ki, forest soil.
[6] P_1 = Kipuka Puaulu, forest soil.
[7] P_2 = Kipuka Puaulu, savannah soil

up much of this ash and redeposited it as a dune at a place where the smooth lava was intercepted by a rough aa flow. The ash-dune now represents an island supporting pioneer vegetation. This process is accumulative since the vegetation, once established, catches more eolian deposits and in turn contributes organic matter, soon forming a moisture- and nutrient-improved habitat that also differs in elevation from its surroundings. It is quite conceivable that such elevated dune ecosystems can be surrounded by subsequent lava flows. Such an occurrence, on a much larger scale, could account for the origin of the kipukas discussed here, although additional evidence to support this hypothesis must be obtained. Also, many, if not most, of the Hawaiian kipukas, such as Kipuka Nene, undoubtedly have developed merely by the disintegration *in situ* of older lavas, the kipuka area being subsequently surrounded by newer flows.

The upper ash deposits in the kipuka soils are more or less horizontal with respect to the present soil surface, a form of deposition which Powers (1948) calls "blanket deposits." The "blanket deposits" in the savannah soil show that there have been at least 9 ash deposits in Kipuka Puaulu since establishment of the thick black horizon (Alb). Not all of these may have been derived from different explosions, but Powers has discovered ash from at least 26 eruptions in the area that occurred later than the big Kilauea ash explosion of 1790. The latest recorded near Kipuka Puaulu was from the 1924 eruption. This shows that the soil is not of one (old) age, but is of several ages from older to younger, and the surface soil may even be much younger than the surrounding rough aa flow, rather than older as indicated by Rock. The surrounding flow is prehistoric, thus at least pre-1778.

Fragments of charcoal were found in both kipukas in the forest soils. They occurred at 70 cm depth in Kipuka Ki and at 80 cm in Kipuka Puaulu. This indicates two facts. First, there was fire in both kipukas at an earlier date in their development; and second, both had woody vegetation growing on them at that time. Although charcoal was not found in the savannah soil, fire may explain its origin. It is interesting that the savannah soil looks quite different from

the forest soils which, in spite of being in two separate kipukas, show much similarity in appearance. Both forest soils are deeply melanized, dark brown in color, and are rather uniformly enriched with organic carbon (Table 1). The savannah soil shows more clearly the parent material, because of less uniform melanization. Here organic carbon content fluctuates greatly between soil horizons. These two patterns, that is, the more uniform color and organic carbon distribution in the forest soils and the greater variation in color and organic carbon distribution in the savannah soil, are undoubtedly associated with past rooting zones. One may assume that a mixed, well-stocked forest occupies the soil volume more uniformly than does a dominantly grass-covered savannah. The grass and ground vegetation roots may have been more restricted to the black horizon zones. Such a concentration in rooting depth was also found at present at the soil surface of the savannah soil. This pattern supports the assumption that the savannah originated after a fire. It is probable that the fire occurred when the 20 cm-thick, black layer, the buried Al horizon (Alb), was at the surface supporting actively growing vegetation, because the charcoal was found right at the lower boundary of this layer in both forest soils (Fig. 2). Therefore, the savannah may be quite old. The C-14 date of the 70 cm-deep charcoal in Kipuka Ki came to 2,170 ± 200 years, *i.e.*, about 220 years B.C.[3]

Analyses of potentially available water, organic carbon, and pH show no significant differences between savannah soil and forest soil in Kipuka Puaulu, so that neither soil water nor nutrient differences can be assumed to be responsible for the difference in vegetation. Moreover, there is no distinctive topographic pattern associated with either type, so that the savannah's origin is not attributable to environmental differences related to topography.

B. Flora

Between November 1963 and March 1965 botanical surveys were made of both kipukas. Voucher specimens have been deposited in the herbarium of the Department of Botany, University of Hawaii, and duplicate specimens in

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[3] Sample GX0394, Geochron Laboratories, Inc.

the herbarium of Hawaii Volcanoes National Park. At the end of this article will be found a check list of the plants found in the two kipukas. It includes also records from Rock (undated, and 1913), and Fagerlund and Mitchell (1944), as well as specimens in the herbaria of Hawaii Volcanoes National Park and the Bernice P. Bishop Museum, Honolulu, Hawaii.

Table 2 summarizes the information provided in the check list. It shows that Kipuka Puaulu now contains, and has contained, significantly more species of vascular plants than has Kipuka Ki. Table 3 provides an analysis of the numbers of species common to both kipukas and of those found only in Kipuka Puaulu or Kipuka Ki. This indicates that, while each kipuka contains species which the other does not, Kipuka Puaulu has a significantly greater number of unique species than does Kipuka Ki.

Thus, the observations recorded in Tables 2 and 3 and in the check list agree with Rock's (1913) observation that there are more species

TABLE 2

NUMBERS OF SPECIES, VARIETIES, AND FORMS OF VASCULAR PLANTS RECORDED FROM KIPUKA PUAULU AND KIPUKA KI

PLANTS	ALL DATA	KIPUKA PUAULU	KIPUKA KI
Total number of spp.	158 (104)*	145 (92)	73 (63)
Native spp.	86 (52)	81 (48)	36 (30)
Native trees	42 (21)	42 (21)	15 (11)
Introduced spp.	72 (52)	64 (44)	37 (33)

* Figures outside parentheses include all spp. ever recorded. Figures within parentheses include all spp. growing naturally in 1963–65.

TABLE 3

DISTRIBUTION OF SPECIES, VARIETIES, AND FORMS OF VASCULAR PLANTS BETWEEN KIPUKA PUAULU AND KIPUKA KI

PLANTS	COMMON TO BOTH KIPUKAS	KIPUKA PUAULU ONLY	KIPUKA KI ONLY
Total number of spp.	60 (51)*	85 (41)	13 (12)
Native spp.	31 (26)	50 (22)	5 (4)
Native trees	15 (11)	27 (10)	— (—)
Introduced spp.	29 (25)	35 (19)	8 (8)

* Figures outside parentheses include all spp. ever recorded. Figures within parentheses include all spp. growing naturally in 1963–65.

in Kipuka Puaulu. The number of native trees now growing in Kipuka Puaulu (21) is almost twice as large as that in Kipuka Ki (11). However, Rock reported in 1913 that there were at least 40 native tree species growing in Kipuka Puaulu. Even allowing for differences of taxonomic opinion, the decrease in number of tree species during the last 50 years appears quite remarkable. In his book, "Indigenous Trees of the Hawaiian Islands," Rock (1913) included 19 photographs of tree species in Kipuka Puaulu. Fifteen of these photographs show bits of landscapes and ground vegetation, which at that time appeared badly abused by cattle grazing. Many areas appear barren or show trampled ground vegetation, and several pictures show broken-down trees. From the photographic record one could assume that the present savannah formation is caused entirely by cattle grazing. However, two photographs show what appear to be sections of the present savannah formation. One of these shows a dense cover of *Pteridium,* which today is also well established in the savannah. Inasmuch as fire has definitely occurred in both kipukas, it is believed that fire may have created openings in the forest that were aggravated and maintained by subsequent cattle grazing. It seems probable that cattle were guided in their grazing habits by this fire-conditioned vegetation pattern, since a denser ground vegetation would be found in the open, coupled with fewer obstacles for the movement of cattle. Increased cloud interception and fog drip in the forest (Ekern, 1964) may also have contributed to maintaining the pattern. This is indicated by the greater current moisture content in the lower profile of the forest soil (Table 1) and the location of the kipukas in a zone of common cloud occurrence (Krajina, 1963).

There are several possible explanations for the larger number of both native and introduced species in Kipuka Puaulu.

1. The larger number of native species in Kipuka Puaulu may be related to:

(a) LARGER AREA. Both kipukas are so much larger than the "minimal" area-size of forest stand communities cited in the literature (Ellenberg [1956] gives 500 m²; Cain and Castro [1959], < 20,000 m² for tropical rain forest), that one may think that size is not a factor.

However, such minimal area calculations are based on the more common species. From the records it is quite clear that the now extinct species were extremely rare. The smaller size of Kipuka Ki can be used, therefore, as one explanation for its smaller number of indigenous species.

(b) GREATER AGE. Rock (1913) believed that Kipuka Ki was more recent in origin than Puaulu, because of the common assumption that an older area would have more species. His idea cannot be disproved from current evidence, but one observation points in the opposite direction. The amount of organic carbon did not decrease in the lower profile of Kipuka Ki, whereas it did so in both soils of Kipuka Puaulu (Table 1). This may indicate vegetative activity at an earlier date in Kipuka Ki as compared with Puaulu.

(c) GREATER DIVERSIFICATION IN HABITATS. This factor in Kipuka Puaulu is not expected from observations made so far. Both kipukas have similar topographic variations and deep, rich soils. Also, the distribution of tree species is not as likely to be affected by small-scale environmental variations as is that of herbaceous plants.

(d) DIFFERENT HISTORY OF DISTURBANCE. Little definite information is available on differences in disturbance-history. We know only that three important disturbance factors operated in both kipukas: fire, cattle grazing, and pig damage. Current pig damage appears to be less in Kipuka Ki. Past cattle grazing also was probably less devastating here. It is possible, however, that fire eliminated a few trees, either directly, or indirectly by competition of more aggressive plants that followed the fire in both kipukas. In this connection, the chance of the smaller, isolated kipuka to be restocked with rare species would be less than that of the larger one, which also may have provided a greater chance of survival of rare tree species simply because of its larger size.

(e) DIFFERENCES IN RAINFALL AND PRODUCTIVITY. It was interesting to find that the current moisture distribution downward in the soils differed between the kipukas. The current soil water content increased considerably in the bottom part of the profile in Kipuka Ki and was higher than in the soils of Kipuka Puaulu,

whereas the upper part of the profile was drier than that of the soils in Kipuka Puaulu. This indicates a different rain shower pattern between the kipukas. This may be a random pattern, however, which then would have no bearing on the total amount received. Except for the lower profile parts (B3 and C2), there was little difference in the amount of organic carbon in the two forest soils, indicating a similar productivity in both kipukas. Thus, the differences in number of species cannot be related to differences in productivity.

2. The larger number of introduced weed species in Kipuka Puaulu may be caused by (a) its greater exposure to man and cattle, and (b) its larger sun-exposed area, which favors the establishment of shade-intolerant weeds. It is interesting that the fewer weed species in Kipuka Ki occupy more ground. Some of them have formed dominant communities.

C. Vegetation

Several obvious plant communities occur under the forest cover. They are represented by native and introduced plants as follows:

NATIVE

    Microlepia association
    Nephrolepis association
    Peperomia patches
    Pipturus shrub strata
    Coprosma thickets

INTRODUCED

    Commelina association
    Rubus penetrans association
    Solanum association
    Dactylis patches
    Commelina-Nephrolepis mixed community

Nephrolepis communities and *Dactylis* patches are common also in open areas. *Coprosma* thickets are characteristic only for Kipuka Puaulu. The *Rubus penetrans* and *Solanum* associations are characteristic for Kipuka Ki. Only one small *Solanum* patch was observed in Kipuka Puaulu. All other associations occur in both kipukas. *Peperomia* patches seem to be established on ground that has been rather recently scarified by pigs, and form there a pioneer community in shaded habitats. Similarly, *Coprosma* thickets are associated with pig scarification,

which is particularly pronounced under larger *Sapindus* trees where the pigs seem to search for their fruits.

SUMMARY AND CONCLUSIONS

1. The soil of both kipukas is derived from several ash deposits. The lower, sloping ones in Kipuka Puaulu differ from the upper ones, which are stratified horizontally.

2. Charcoal was found in both kipukas under forest in association with a buried, black surface horizon, at 70 cm depth in Kipuka Ki and at 80 cm in Puaulu.

3. The C-14 analysis of the 70 cm-deep charcoal in Kipuka Ki indicates that a fire occurred at about 220 B.C.

4. The forest soils of both kipukas are uniformly melanized, showing considerable megascopic similarity, and differ markedly from the savannah soil, which showed melanization restricted to narrow layers and which exposed a clear parent material stratification.

5. The soil parameters tested indicated no significant differences between the forest soil and the savannah soil of Kipuka Puaulu in terms of soil water, organic carbon, and pH.

6. The forest soils of the kipukas differ only in current soil moisture distribution and organic carbon content of the lower horizons (B3 and C2).

The work so far is only an introduction to the plant ecology of Hawaiian kipukas and points to the need for the following further research:

1. Analysis of photographs. It would be profitable to examine all photographs Rock made of Kipuka Puaulu and, if possible, to identify some spots for rephotographing. This could reveal certain interesting successional changes over the last 50 years.

2. Current observation indicates reoccupation of the savannah by forest. This appears to be accomplished by sucker growth of *Acacia koa*. Invasion of trees by seed seems practically impossible. It would be interesting to study the rate of reinvasion, now, when there is no more interference by cattle.

3. Studies of cloud interception. Differences in soil water supply as a result of fog drip should be investigated, to determine the role

this environmental factor plays in influencing the rate of reinvasion of forest into the savannah.

4. Measuring pig damage. Current observation indicates that pigs affect the forest vegetation in two ways. (a) By scarifying the surface, they eliminate ground vegetation and provide ideal seed beds for tree seed germination of that which is left. Many formerly pig-scarified areas seem to come back in thickets of tree seedlings of *Sapindus* and *Coprosma.* (b) During periods of food scarcity or over-population pigs seem to gnaw away the bark of trees, particularly of *Coprosma,* thus damaging them severely, e.g., by providing entrance avenues for pathogens. The food habits of pigs should be studied in connection with population counts to explain their influence on vegetation patterns.

5. Quadrat studies of vegetation patterns. These should be done in particular with *Peperomia,* as a probable native pioneer on pig-scarified ground; with *Commelina* and *Nephrolepis* mixed associations, to determine whether *Commelina* takes over the habitats occupied by the native fern, *Nephrolepis*; and with the two weed communities formed by *Rubus penetrans* and *Solanum pseudocapsicum,* to determine their effect on the native *Microlepia* association.

6. An ecological survey of all kipukas and their surroundings should be made in an attempt to assess their development in succession and their influence on the vegetation of the surrounding more recent volcanic material.

CHECK LIST OF PLANTS IN THE KIPUKAS

This check list includes all of the vascular plant species of Kipuka Puaulu and Kipuka Ki as of May 1965. The symbols used are: * = native Hawaiian species; # = native tree; + = growing, apparently naturally, in kipuka in 1963–65; a = growing in kipuka in 1963–65 only as individuals recently planted by National Park Service; b = specimens, collected between 1930 and 1960, in herbaria at Hawaii Volcanoes National Park or B. P. Bishop Museum, but species not found growing in kipuka in 1963–65; c = reported by Fagerlund and Mitchell (1944), but no specimens available; d = reported by Rock (undated, and 1913), but no more recent specimens available.

SPECIES	KIPUKA PUAULU	KIPUKA KI
PTERIDOPHYTA		
ASPIDIACEAE		
* Athyrium sandwichianum Presl.	+	
Cyclosorus dentatus (Forsk.) Ching	+	
C. parasiticus (L.) Farwell		+
* Cyrtomium caryotideum (Wall.) Presl.	+	
* Dryopteris glabra (Brack.) Kuntze	b	
* D. hawaiiensis (Hillebr.) Christ	+	+
* D. latifrons (Brack.) Kuntze	+	
* D. paleacea (Swartz) Christensen	+	+
* Elaphoglossum conforme (Swartz) Schott		b
ASPLENIACEAE		
* Asplenium adiantum-nigrum L.	+	
* A. cf. caudatum Forst. f.	+	+
* A. macraei Hook. et Grev.	c	b
BLECHNACEAE		
* Sadleria cyatheoides Kaulf.	+	+
DAVALLIACEAE		
* Nephrolepis exal·cta (L.) Schott	+	+
POLYPODIACEAE		
* Pleopeltis thunbergiana Kaulf.	+	+
PSILOTACEAE		
* Psilotum nudum (L.) Griseb.	+	
PTERIDACEAE		
* Cibotium chamissoi Kaulf.	d	
* C. glaucum (Smith) Hook. et Arn.	+	+
* Coniogramme pilosa (Brack.) Hieron.		+
* Microlepia setosa (Smith) Alston	+	+
* Pellaea ternifolia (Cav.) Link	b	

SPECIES	KIPUKA PUAULU	KIPUKA KI
* Pteridium aquilinum (L.) Kuhn		+
* Pteris cretica L.	+	+
* P. excelsa Gaud.	+	
MONOCOTYLEDONAE		
COMMELINACEAE		
Commelina diffusa Burm.	+	+
CYPERACEAE		
* Carex macloviana D'Urv. var. subfusca (Boott) Kükenth.	+	+
* C. wahuensis C. A. Meyer var. rubiginosa R. W. Krauss	+	
Cyperus brevifolius (Rottb.) Hassk.	+	+
* C. hillebrandii Boeck.	b	
* C. polystachyus Rottb.		+
GRAMINEAE		
Agrostis retrofracta Willd.		+
Anthoxanthum odoratum L.	+	+
Briza minor L.	b	
Bromus commutatus Schrad.	c	
B. rigidus Roth	c	+
B. secalinus L.	b	
B. unioloides (Willd.) H.B.K.	+	+
Cynodon dactylon (L.) Pers.	+	+
Dactylis glomerata L.	+	+
Digitaria pruriens (Trin.) Buese	d	
Festuca dertonensis (All.) Asch. et Graebn.	b	
Holcus lanatus L.	+	
* Panicum tenuifolium Hook. et Arn.	b	
Paspalum conjugatum Berg.	+	
P. dilitatum Poir.	+	+
P. urvillei Steud.		+
Poa annua L.	+	
P. pratensis L.		+
Setaria geniculata (Lam.) Beauv.	+	

SPECIES	KIPUKA PUAULU	KIPUKA KI
Sporobolus africanus (Poir.) Robyns et Tournay	+	
Stenotaphrum secundatum (Walt.) Kuntze	b	
Unidentified grass	+	+
IRIDACEAE		
X *Tritonia crocosmaeflora* Lemoine	+	
LILIACEAE		
Cordyline terminalis (L.) Kunth	+	
* *Smilax sandwicensis* Kunth	d	
ZINGIBERACEAE		
Hedychium coronarium Koenig	+	
DICOTYLEDONAE		
AMARANTHACEAE		
* # *Charpentiera obovata* Gaud.	+	a
APOCYNACEAE		
* *Alyxia olivaeformis* Gaud.	+	
* # *Ochrosia sandwicensis* A. Gray	a	
ARALIACEAE		
Brassaia actinophylla F. Muell.	b	
* # *Cheirodendron trigynum* (Gaud.) Heller	+	
CELASTRACEAE		
* # *Perrottetia sandwicensis* A. Gray	+	
COMPOSITAE		
Achillea millefolium L.	b	
Bidens pilosa L.	+	+
Cirsium lanceolatum (L.) Hill.	+	
Erigeron albidus (Willd.) A. Gray	b	
E. canadensis L.	b	
Hypochaeris radicata L.	+	+
Senecio sylvaticus L.		c
Sonchus asper L.	+	+
S. oleraceus L.	c	

SPECIES	KIPUKA PUAULU	KIPUKA KI
CONVOLVULACEAE		
* *Ipomoea indica* (Burm.) Merr.	+	+
CRUCIFERAE		
Lepidium virginicum L.	b	
Sisymbrium officinale (L.) Scop.		b
EPACRIDACEAE		
* *Styphelia tameiameiae* (Cham.) F. Muell.	+	+
EUPHORBIACEAE		
Aleurites moluccana (L.) Willd.	a	
FLACOURTIACEAE		
* # *Xylosma hawaiiensis* Seem. var. *hillebrandii* (Wawra) Sleumer	b	
GENTIANACEAE		
Centaurium umbellatum Gilib.	b	
GERANIACEAE		
Geranium carolinianum L. var. *australe* (Benth.) Fosb.	+	+
HYPERICACEAE		
Hypericum mutilum L.	+	
LABIATAE		
Mentha sp.	+	
LAURACEAE		
Persea americana Mill.	+	
LEGUMINOSAE		
* # *Acacia koa* A. Gray	+	+
Desmodium uncinatum (Jacq.) DC.	+	+
* # *Sophora chrysophylla* (Salisb.) Seem.	+	+
LOBELIACEAE		
* # *Clermontia hawaiiensis* (Hillebr.) Rock	d	
* # *Clermontia* sp.	a	
LORANTHACEAE		
* *Korthalsella complanata* (Van Tiegh.) Engl.	+	
LYTHRACEAE		
Cuphea carthaginensis (Jacq.) Macbride	b	
Lythrum maritimum H. B. K.	+	+

SPECIES	KIPUKA PUAULU	KIPUKA KI
MALVACEAE		
* # Hibiscadelphus giffardianus Rock	a	a
* # H. hualalaiensis Rock	a	
* # Kokia rockii Lewt.	a	
Modiola caroliniana (L.) G. Don	+	+
MENISPERMACEAE		
* Cocculus ferrandianus Gaud.	+	
MORACEAE		
Ficus carica L.	b	
MYOPORACEAE		
* # Myoporum sandwicense A. Gray var. fauriei (Lev.) Kraenzl.	+	+
MYRSINACEAE		
* Embelia pacifica Hillebr.	+	
* # Myrsine lessertiana A. DC.	+	+
MYRTACEAE		
* # Metrosideros polymorpha Gaud.	+	+
Psidium cattleianum Sabine	+	
P. guajava L.		+
NYCTAGINACEAE		
* # Heimerliodendron brunonianum (Endl.) Skottsb.	+	a
OLEACEAE		
* # Osmanthus sandwicensis (A. Gray) Knobl.	+	+
ONAGRACEAE		
Oenothera stricta Ledeb.		+
OXALIDACEAE		
Oxalis corniculata L.	+	+
PAPAVERACEAE		
* Argemone glauca L. ex Pope	b	
PASSIFLORACEAE		
Passiflora ligularis Juss.	+	
PHYTOLACCACEAE		
* Phytolacca sandwicensis Endl.		+

SPECIES	KIPUKA PUAULU	KIPUKA KI
PIPERACEAE		
* Peperomia cookiana C. DC.	+	+
* P. hypoleuca Miq.		+
* P. leptostachya Hook. et Arn.	b	
* P. reflexa Dietr. var. reflexa	c	
* P. reflexa Dietr. var. parvifolia C. DC.	+	+
PITTOSPORACEAE		
* # Pittosporum hosmeri Rock var. longifolium Rock	a	
* # P. hosmeri Rock var. saint-johnii Sherff	a	
PLANTAGINACEAE		
Plantago lanceolata L.	+	+
POLYGONACEAE		
Rumex acetosella L.	+	+
PRIMULACEAE		
Anagallis arvensis L.	c	+
RANUNCULACEAE		
Ranunculus muricatus L.	c	b
RHAMNACEAE		
* # Alphitonia ponderosa Hillebr.	a	
ROSACEAE		
Fragaria vesca L. forma alba (Ehrh.) Rydb.	+	+
Prunus persica (L.) Batsch	+	c
* Rubus hawaiiensis A. Gray	+	
* R. macraei A. Gray	d	
R. penetrans L. H. Bailey	+	+
R. rosaefolius Smith	+	+
RUBIACEAE		
* # Coprosma cymosa Hillebr.	c	
* # C. rhynchocarpa A. Gray	+	+
* # Gouldia terminalis (Hook. et Arn.) Hillebr. var. antiqua Fosb. forma antiqua	c	

SPECIES	KIPUKA PUAULU	KIPUKA KI
* # G. terminalis (Hook. et Arn.) Hillebr. var. antiqua Fosb. forma acuta Fosb.	+	
* # G. terminalis (Hook. et Arn.) Hillebr. var. konaensis Fosb. forma konaensis	b	
* # Psychotria hawaiiensis (A. Gray) Fosb. var. hillebrandii (Rock) Fosb.	+	+
RUTACEAE		
* # Fagara dipetala (Mann) Engl. var. geminicarpa (Rock) St. John	+	
* # F. mauiense (Mann) Engl. var. anceps (Rock) St. John	b	
* # F. mauiense (Mann) Engl. var. anceps (Rock) St. John forma petiolulatum (Rock) St. John	b	
* # Fagara sp.	d	
* # Pelea hawaiiensis Wawra var. gaudichaudii (St. John) Stone	+	
* # P. puauluensis St. John	+	
* # P. zahlbruckneri Rock	+	
* # Pelea sp.	d	
* # Pelea sp.	d	
* # Pelea sp.	d	
SAPINDACEAE		
* # Dodonaea viscosa (L.) Jacq. var. spathulata (Sm.) Benth.	+	+
* # Sapindus saponaria L.	+	+
SCROPHULARIACEAE		
Linaria canadensis (L.) Dumont	b	
Veronica plebeia R. Br.	+	+
V. serpyllifolia L.	+	
SOLANACEAE		
* # Nothocestrum breviflorum A. Gray	b	b
* # N. longifolium A. Gray	d	

SPECIES	KIPUKA PUAULU	KIPUKA KI
Physalis peruviana L.	+	+
Solanum pseudocapsicum L.	+	+
THYMELAEACEAE		
* Wilkstroemia phillyreaefolia A. Gray	b	
TROPAEOLACEAE		
Tropaeolum majus L.	+	
UMBELLIFERAE		
Hydrocotyle sibthorpioides Lam. var. oedipoda Deg. et Greenwell	+	
URTICACEAE		
* # Pipturus hawaiiensis Lev.	+	+
* # Urera sandwicensis Wedd.	+	
VERBENACEAE		
Verbena litoralis H. B. K.	+	+

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PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL
AND PHYSICAL SCIENCES OF THE PACIFIC REGION

UNIVERSITY OF HAWAII PRESS

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PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL
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CONTENTS

CONTENTS (*continued*)

A Study of the Source Mechanism of the Alaska Earthquake and Tsunami of March 27, 1964

Part I. Water Waves[1]

George Pararas-Carayannis

ABSTRACT: The geologic history and the general geomorphology of the area affected by the March 27, 1964 Alaska earthquake are given. The tsunami-generating area is determined and the extent of crustal displacement and the limits of the areas of subsidence and uplift, as revealed by geologic evidence, are discussed. The dimensions of this tsunami-generating area, its volume of crustal displacement, and the energy associated with the tsunami are calculated. Wave activity within and outside the generating area and the possible generating mechanisms for the tsunami are discussed. A wave refraction diagram of the Alaska tsunami for the north Pacific Ocean area is presented in Figure 6.

THE ALEUTIAN ISLAND ARC and the Aleutian Trench extend for 2800 km from Kamchatka to south-central Alaska along remarkably smooth curves which are convex toward the south (Fig. 1). The Arc forms the Alaska Peninsula and, according to Wilson (1954), intersects, north of Cook Inlet, a second tectonic arc that extends northward from the vicinity of the Wrangell Mountains. However, Plafker (1965) regards this second segment as a continuation of the Aleutian Arc. Where the trench impinges on Alaska it loses its identity, although an offshore range of seamounts suggests it may once have extended around to the south to parallel the continental slope, as postulated by Menard and Dietz (1951). Concavity in the former shape of the trench on its eastern segment is also suggested by the sedimentary arc defined by Wilson (1954), which embraces Kodiak Island and the Kenai Peninsula. As shown by Wilson, such concavity is to be expected where two arcs meet at an acute angle, as is well exemplified where the Aleutian and Kuril-Kamchatka arcs intersect. It is also quite possible that large horizontal movements of crustal blocks have helped to change the shape of the Trench and Arc on their eastern segments. However, no such evidence was found in a field study following the Good Friday earthquake (Berg et al., in preparation).

The nature of the termination of the eastern segment of the Aleutian Trench is obscured by thick sediments washed in from the continental shelf against which it abuts offshore from Cape Suckling. The sediments are of geosynclinal-dimensions in the sedimentary arc on Kodiak Island (Menard and Dietz, 1951) and as shown by drilling on the Kenai Peninsula. Woollard et al. (1960) show there is geophysical evidence for at least 7 km of sediments in Cook Inlet, a graben separating the primary arc from the offshore sedimentary arc. Sediment is about 2 km thick off Kodiak Island along the Aleutian Trench, thinning out to about 0.7 km south of Unimak Island in the deep water area, according to seismic measurements by Shor (1962).

THE GENERATING AREA OF THE ALASKA TSUNAMI

According to Van Dorn (1964), the tectonic dislocations associated with the Alaska earthquake of March 27, 1964 ranged over a distance of 800 km, from the upper portion of Prince William Sound to southwest of the Trinity Islands. The dislocations follow a dipole pattern of positive and negative displacements on either side of a zero-line which, intersecting the east coast of Kodiak Island, continues northeast to the western side of Prince William Sound. There, changing direction, it

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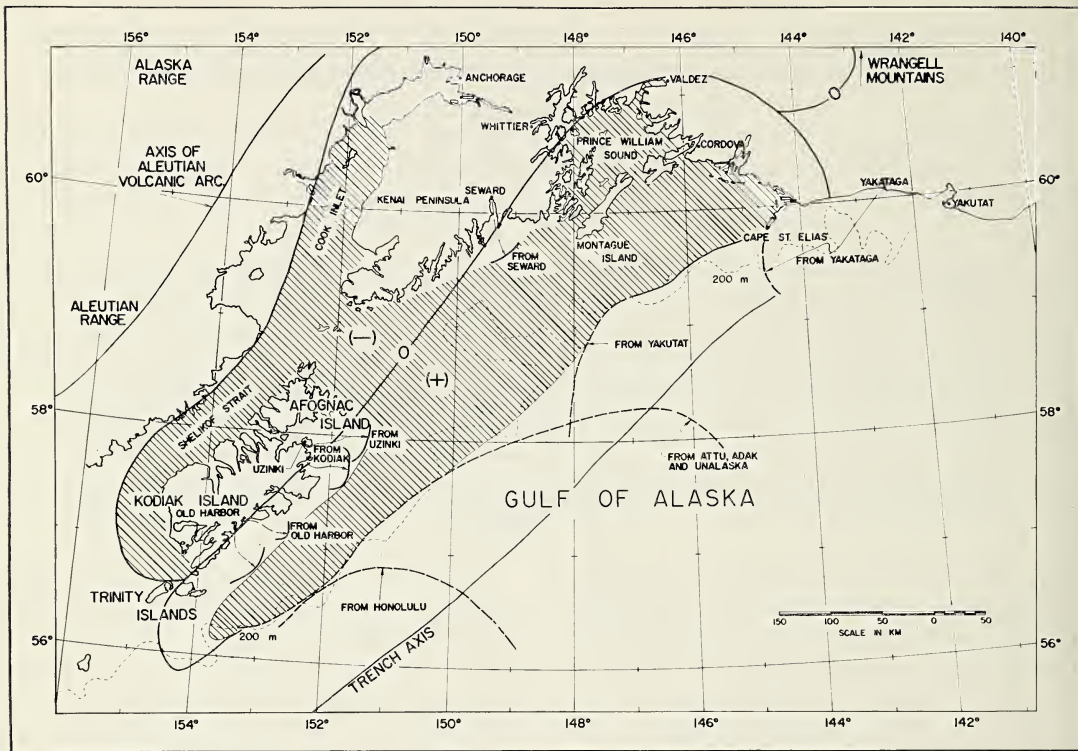
FIG. 1.   Generating area of the Alaska tsunami. *Crosshatched area* indicates (−) area of subsidence and (+) area of uplift. *Heavy dashed lines* indicate the backward-refracted wave fronts. *Solid line marked by a zero* is the axis of rotation (no elevation change). *Other solid lines* indicate tectonic axes.

runs east along the upper part of the sound. The line roughly parallels the Aleutian Trench axis and separates the Kodiak geosyncline from the shelf geanticline.

The areas north and west of this line have undergone negative elevation changes, whereas the east and south underwent positive changes. An extensive pattern of positive surface dislocations under the sea is suspected to lie east of the island of Kodiak and along the continental shelf bordering the Gulf of Alaska. The extent of these dislocations still needs to be confirmed by detailed bathymetric surveys of the area, although large positive displacements have been observed as far south as Middleton Island and southwest to Sitkinak Island. Wave refraction studies, described here, also strongly indicated that the tsunami-generating area was mainly in the belt of uplift and included a large segment of the continental shelf and slope.

The zone between the known areas of tec-

tonic uplift closely corresponds to a major crustal fault defined by crustal seismic measurements conducted by the Department of Terrestrial Magnetism of the Carnegie Institution of Washington (Woollard et al., 1960). In view of the shallowness of the earthquake (20 km), it was concluded that the crustal dislocations occurred alongside a zone of tilting or a surface rupture (Grantz et al., 1964), but a survey of the area failed to identify such a feature. The focal depth corresponds, however, to the base of the granitic layer defined by Woollard's analysis of the crustal measurements made by the Carnegie Institution.

The total area of tectonic displacements associated with the Alaska earthquake of March 27, 1964 is estimated to be approximately 215,000 km^2. This is the largest area known to be associated with a single earthquake within historic time.

The magnitude of the Alaska earthquake was estimated to be from 8.4 to 8.75, which

is greater than the 1906 San Francisco earthquake (8.3), and equal to or greater than the 1960 Chile earthquake (8.4). The epicenter of the earthquake was at 61.05°N, 147.7°W (USCGS, 1964), near the east shore of Unakwik Inlet in northern Prince William Sound.

Geological investigations have defined the land areas affected by the earthquake. To the east, the zone of deformation appears to die out between the Bering Glacier and Cape Yakataga. The northwestern limit of tectonic changes extends at least to the west side of Shelikof Strait and Cook Inlet (Plafker, 1965). The north inland limit is known only along the highway connecting Valdez and Fairbanks; it appears to extend in a northeasterly direction to the vicinity of the Wrangell Mountains, and quite possibly into the Alaska Range.

The area of uplift covers about 105,000 km² and extends from southern Kodiak Island northeast to Prince William Sound. It includes the southern and eastern parts of Prince William Sound, the coastal area as far east as the Bering Glacier, and the continental shelf and part of the slope to a depth contour of approximately 200 m. The maximum uplift on land was 10 m at the southwest end of Montague Island, but is suspected to have been considerably more offshore. Uplift also occurred along the extreme southeastern coasts of Kodiak Island and Sitkalidak Island, and part or all of Sitkinak Island. The maximum measured uplift of Sitkalidak Island was 0.4 m. The estimated uplift of Sitkinak Island was from 0.35 to 0.65 m and possibly as much as 1.5 m (Plafker, 1965).

The area that subsided included the northern and western parts of Prince William Sound, the western segment of the Chugach Mountains, portions of the lowlands north of them, most of the Kenai Peninsula, and almost all of the Kodiak Island group. This area of subsidence covers approximately 110,000 km², and is 800 km long and 150 km wide. Plafker (1965) estimates that the volume of crust that has been depressed below its pre-earthquake level is about 115 km³.

The seaward limits of the earthquake and the tsunami-generating area were determined by means of a series of refraction diagrams based on Snell's Law of Refraction using the velocity equation for shallow water waves, $C = \sqrt{gd}$.

Such a method of preparing refraction diagrams has shown good results, especially if carried out on large-scale charts with detailed bathymetry (Johnson, O'Brien, and Isaacs, 1948).

In constructing the refraction diagrams for the Alaska tsunami, the marigrams of different tide gauge stations around the Pacific were consulted and the total travel time of the first wave at each station was determined. Then refraction diagrams were constructed toward the earthquake area from each tide gauge station in lengths of time equal to the calculated travel time for that station. It was assumed that the last wave front in each refraction diagram would correspond to a point on the boundary of the generating area, and if enough refracted wave fronts from different stations were plotted, an envelope defining the tsunami-generating area could be drawn.

Wave fronts were refracted from Yakatat, Cape Yakataga, Seward, Uzinki, Kodiak, Old Harbor, Unalaska, Adak, Attu, and Honolulu. The last front of each of the refracted waves is shown by a heavy dashed line in Figure 1. The seaward boundary of the generating area is near the 200-m depth contour which defines the edge of the continental shelf. Maximum displacement of the ocean floor occurred along the continental shelf, from an area southeast of Kodiak Island, to an area close to Cape St. Elias south of the island of Kayak (Fig. 1). Geologic evidence, however, has shown positive land displacements as far north as Cape Suckling and as far east as the Bering Glacier. It is quite probable, therefore, that the tsunami-generating area extended farther to the northeast, although waves generated in such shallow water would reach tide gauges much later and their origin would not be identifiable.

Unfortunately, this same wave refraction technique could not be used to define the northern and western boundaries of the main tsunami-generating area, because conditions in Prince William Sound and elsewhere along the coast of Alaska were further complicated by local tsunamis, oscillations, and surge. In addition, no tide gauge stations were operating in the area, and personal accounts were conflicting as to arrival times of the different waves.

The northward limit is assumed to be restricted by the land boundaries, and the western

limit to extend to the west side of Shelikof Strait and Cook Inlet.

In estimating the travel time of the tsunami, corrections were made for the delay at the island of Kodiak in the arrival of the ground shocks from Prince William Sound. These corrections ranged from 1 minute to 6 minutes and were based on the fact that the Navy Weather Central on the island of Kodiak listed the time of the principal shock in Prince William Sound as 6 minutes later than the time listed by the U. S. Coast and Geodetic Survey. This would imply that the wave front generated on the northeast side of the disturbance area had a 6-minute head start on the wave front generated southeast of Kodiak.

The tsunami-generating area covers an area 700 km long by 150 km wide, a total of about 105,000 km². The volume of the uplifted crust along the continental shelf is about 96 km³. The energy associated with the tsunami has been estimated by Van Dorn (1964) to be of the order of 2.3×10^{21} ergs. This estimate is based on the source dimensions of an area 240 nautical miles by 100 nautical miles and an uplift of 1.8 m (6 ft) at the northeastern end of this area and zero at the southwestern end. This estimate, however, is considered low because the generating area had dimensions that were larger than those estimated by Van Dorn.

Using our source dimensions, and assuming that the total energy was equal to the potential energy of the uplifted volume of water, the total energy for the tsunami in the Gulf of Alaska was calculated as follows:

$$E_t = \frac{1}{6}\rho g h^2 A$$

$$= \frac{1}{6}(1.03)(.980)(10^3)(10^4)(1.83^2)(1.5$$

$$\times 10^7)(7 \times 10^7) = 5.88 \times 10^{21} \text{ ergs}$$

where

$E_t = E_p$ = total energy
ρ = 1.03 g/cm³ = density
g = 980 cm/sec²
h = height of displacement = 1.83 m
A = area
1 erg = g cm² sec⁻²

The waves generated in the Gulf of Alaska were of an unusually long period, on the order

of an hour or more. Their energy radiation was preferentially directed toward the southeast and this is why more damage was done to the North American coast than anywhere else east or south of the generating area. This preferential directivity of energy radiation can be attributed to the orientation of the tectonic displacements along the continental shelf of the Gulf of Alaska, and the long period of the waves can be related to the long seiche period of the shallow shelf.

According to Japanese seismologists (Iida, 1958), the generating area of a tsunami roughly corresponds to the distribution of the major aftershocks. This appears to be indeed the case in the Gulf of Alaska.

There were 52 aftershocks of the Alaska earthquake. The largest had a magnitude of 6.7. The aftershocks occurred in an area from about 15 km north of Valdez to about 55 km south of Trinity Islands, and were heavily concentrated on the northeast and the southwest of the uplifted region (USCGS, 1964), which also was the main tsunami-generating area.

The vast area of tectonic movements indicates that wave crests were generated along one or more line sources from the region of maximum uplift. Thus, the shores of the Kenai Peninsula were struck within 20 minutes after the start of the earthquake, and those of Kodiak Island, within 34 minutes.

Unfortunately, the violence of the earthquake left south-central Alaska without a tide gauge in operation. The only reliable record from the generating area is the one that was obtained by personnel of the U. S. Navy Fleet Weather Station at Kodiak; it is shown in Figure 2. This record has been corrected for the 1.7-m (5.6-ft) submergence of the area.

Outside the immediate generating area, the record of Cape Yakataga, as constructed from the personal account of C. R. Bilderback, a resident of the area, is the next most reliable record. This record is the only one obtained outside the generating area that shows an initial drop in the water level (Berg et al., in preparation). Withdrawal of the water immediately following the earthquake has been reported from Kayak, Middleton, and Hinchinbrook islands, as well as from Rocky Bay and Nuka Bay, at the end
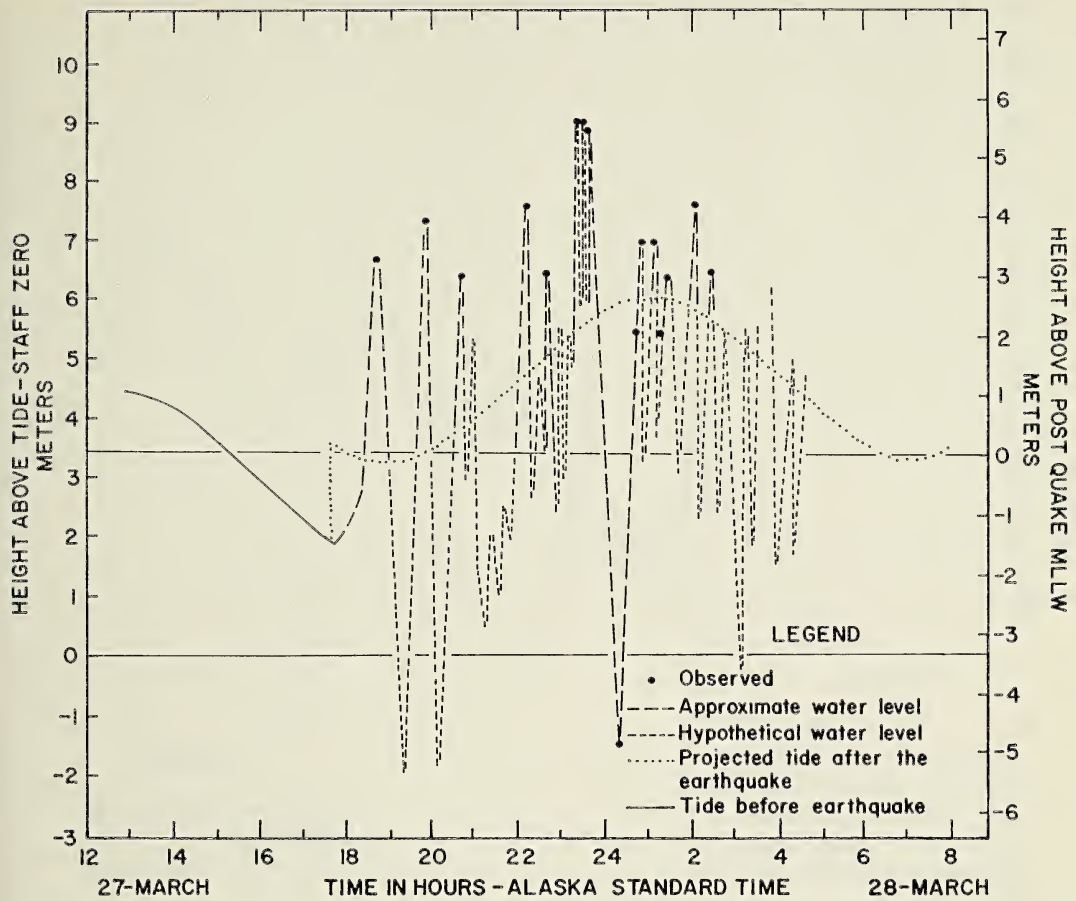
Fig. 2. Diagram of wave activity at Women's Bay, Kodiak Island. (From visual observations made at Marginal Pier, Nyman Peninsula.)

of the Kenai Peninsula, but these islands are inside the generating area.

Yakatat, a coastal town 170 km southeast of Cape Yakataga, had a tide gauge in operation, and the marigram shows that a positive wave arrived first (Fig. 3).

It is quite possible, therefore, that the first waves to arrive at Cape Yakataga had a different origin from that of the first waves to arrive at Yakatat. It could very well be that the Cape Yakataga waves traveled over the shallow portion of the shelf, whereas the Yakatat waves came from the open ocean.

An interesting aspect of these two records is that of the difference in amplitude and period of the first waves to arrive at these two sites—which also supports the hypothesis of difference in origin (see Figs. 3 and 4).

TSUNAMI GENERATED IN PRINCE WILLIAM SOUND

The shallow continental shelf and the islands bordering the southern side of Prince William Sound, as well as the pattern of crustal displacements, confined the waves generated in this area to the Sound itself; very little energy escaped this closed region. Most of the energy was expended in the narrow, deep fjords of the Sound, creating catastrophic waves and setting up resonating oscillations and surges that lasted for hours. In certain places maximum inundation occurred 5 or 6 hours later, at high tide. At Valdez, for example, the third wave came in at 2300, March 27, and the fourth one at 0145, March 28 (Brown, 1964). This last wave took the form of a tidal bore and inundated the
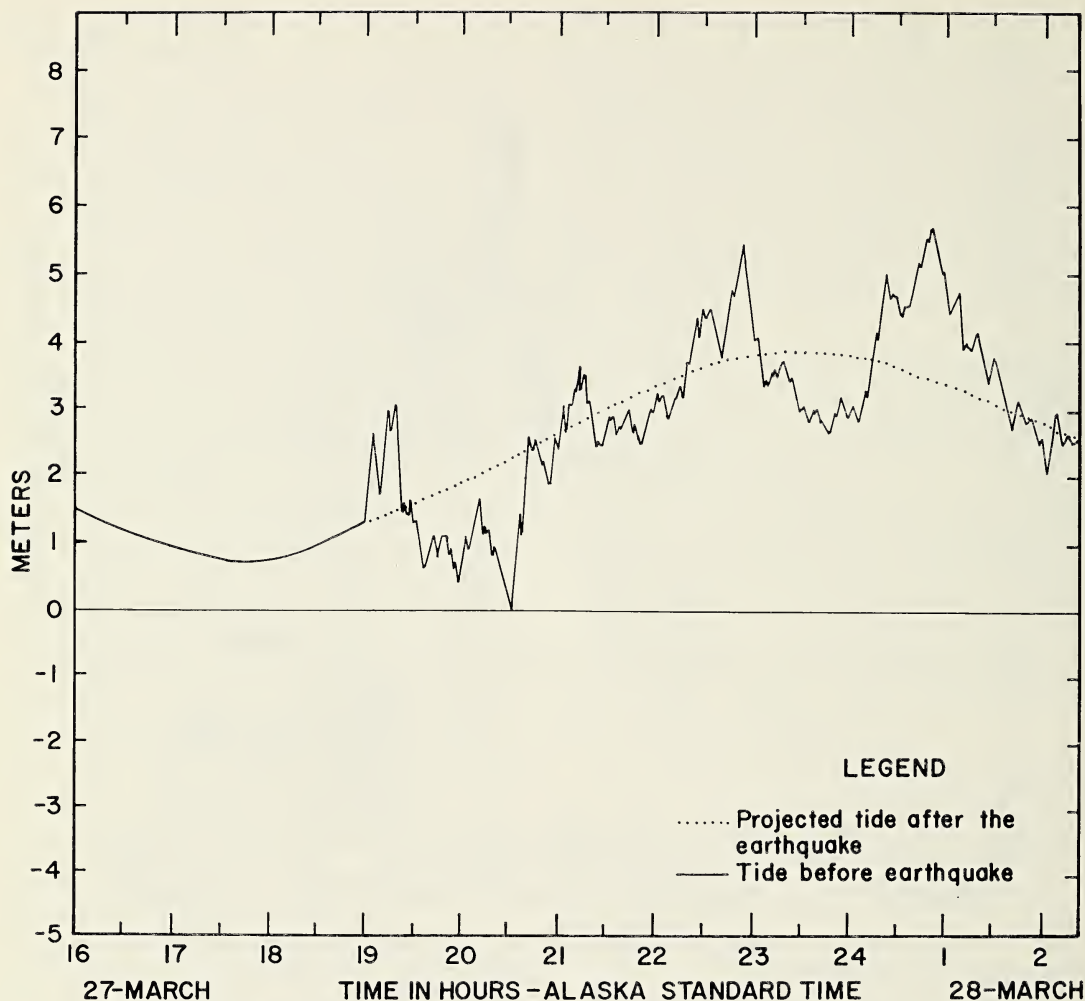
FIG. 3.   Marigram of wave activity at the town of Yakutat.

downtown section of Valdez, ruining almost all the merchandise in the stores. These waves could not have come from the generating area outside Prince William Sound because if this were so, it would have taken them only 34 minutes to reach Valdez. It is more likely, then, that the waves at Valdez arrived in resonance at high tide, from the immediate area of Port Valdez.

Maximum positive crustal displacement in Prince William Sound occurred along the northwest coast of Montague Island and in the area offshore. These earth movements caused a gradient in hydrostatic level and the resulting short-period wave raced through Knight Island Passage within 10 minutes and on toward Che-

nega Island, inundating the village of Chenega to an elevation of 15.5 m and completely destroying it. This same wave continued north through Knight Island Passage and inundated Perry and Naked islands, but to lesser heights (Berg et al., in preparation).

Bathymetric surveys by the USCGS (1964) in the area off Montague Island and at the north end of Latouche Island revealed a number of large submarine slides. It is possible, therefore, that the combination of submarine slides and the tilting of the ocean floor due to uplift created the solitary wave reported at Chenega village and at Perry and Naked islands.

A second wave about 40 m high (125 ft) was reported coming out of the Valdez Narrows
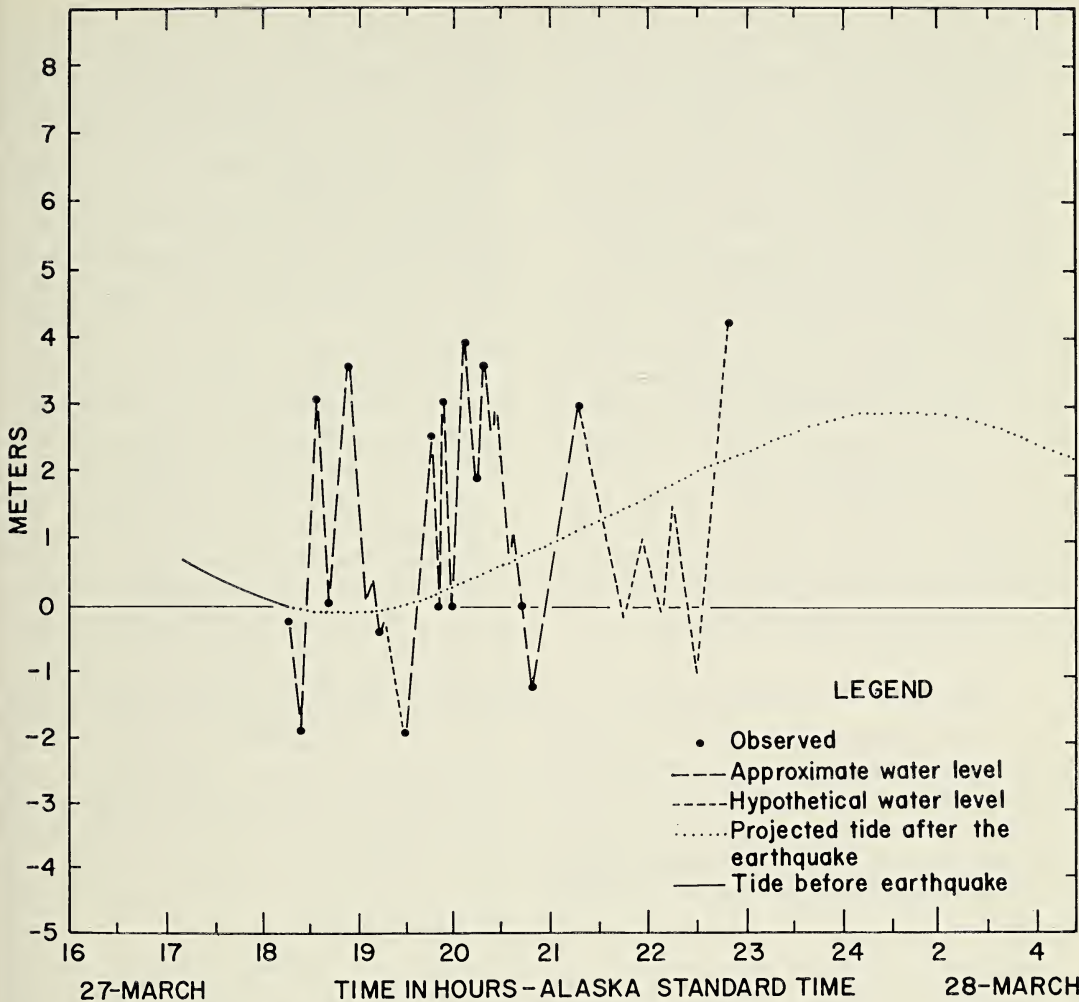
Fig. 4. Diagram of wave activity at Cape Yakataga.

and spreading across the Sound (Plafker and Mayo, 1965). This wave was caused by slumping of the glacial deltas in Port Valdez which had been shaken loose by the force of the earthquake.

TSUNAMI MECHANISM

Most tsunamis result from earthquakes having focal depths of less than 60 km. Iida (1958) has derived an empirical relation giving the maximum focal depth H (in km) for an earthquake of magnitude M which has resulted in a detectable tsunami:

$$M = 6.42 + 0.01 \; H \qquad (1)$$

where M is the Richter magnitude given by

$$\log \; E(\text{ergs}) = 11.8 + 1.5 \; M \qquad (2)$$

The focal depth of the Alaska earthquake was about 20 km. This was shallow enough to create tsunami waves even though the epicenter of the main shock was as much as 100 km inland from the coast. A number of shallower aftershocks over a large area ranging from Hinchinbrook Island to southeast Kodiak Island indicate that crustal movements over a wide area were involved. Undoubtedly these shallow aftershocks created smaller waves that could not be separated, in the tide gauge records, from reflections of the initial tsunami.

If the tsunami waves that hit the island of Kodiak were the result of crustal movements only, then the first wave could be expected to

be the highest, at least within the generating area. At Uzinki, Kodiak City, Women's Bay, and elsewhere on the island of Kodiak, however, the third and fourth waves were the highest. A theory of generation from a single pattern of crustal deformation is therefore not satisfactory here. Such factors as reflection from coastal boundaries, wave interaction, and resonance should be taken into consideration.

Slumps or avalanches, similar to the ones that occurred in Prince William Sound, are usually localized; they can produce no large tsunamis that would travel across wide portions of the ocean. According to Wiegel (1954), not more than 2% of the potential energy of a falling or sliding body is converted into wave energy. In Prince William Sound, however, slumping and sliding when added to tectonic movements created tsunami waves of very large energy, but their effect was catastrophic only locally; very little of the energy escaped the Sound.

SUMMARY AND CONCLUSIONS

The Alaska earthquake of March 27, 1964 affected an area of approximately 215,000 km², extending from the Wrangell Mountains at the northeast to the Trinity Islands in the southwest, and from the west side of Shelikof Strait and Cook Inlet east to the vicinity of the Bering Glacier.

Geologic evidence has revealed a dipole pattern of positive and negative tectonic movements resulting from this earthquake. The area of subsidence covers approximately 110,000 km² and the volume of crust that has been depressed below its pre-earthquake level is about 115 km³.

The area of uplift covers about 105,000 km² and includes the southern and eastern parts of Prince William Sound, the coastal area as far east as the Bering Glacier, and a great part of the continental shelf and slope bordering the Gulf of Alaska.

The seaward limits of the area affected by the Alaska earthquake and the tsunami-generating area were determined by means of a series of wave refraction diagrams as shown in Figure 5, based on Snell's Law of Refraction. The tsunami-generating area covers 140,000 km² and includes the whole of the region of uplift and part of the region of subsidence. It extends from the Trinity Islands to the Bering Glacier and includes Shelikof Strait, Cook Inlet, and the continental shelf bordering the Gulf of Alaska to a depth of approximately 200 m. The total volume of displaced material in the tsunami-generating area was estimated to be 120 km³, and the energy associated with the tsunami was calculated to be in the order of 6×10^{21} ergs.

As a result of this work the following conclusions are drawn:
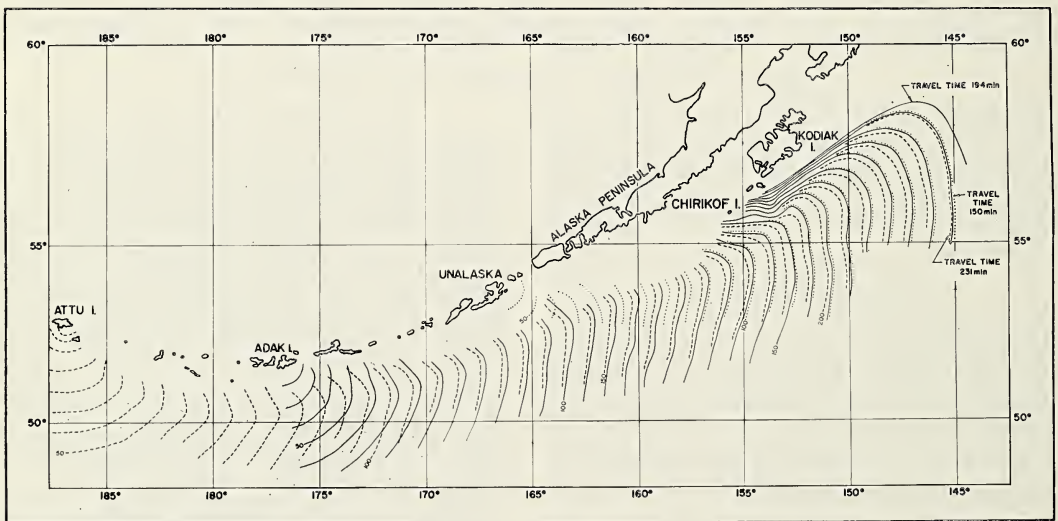
FIG. 5. Diagram of wave fronts refracted toward the earthquake area from Attu Island (*dashed line*), Adak Island (*solid line*), and Unalaska Island (*dotted line*).

1. Two main tsunami-generating areas can be distinguished: one along the continental shelf bordering the Gulf of Alaska; the other in Prince William Sound.

2. The main generating area in the Gulf of Alaska roughly corresponds to the geographic distribution of the major aftershocks.

3. The energy of the tsunamis generated in Prince William Sound was expended inside the Sound; not much energy escaped this closed region.

4. The long period of the waves generated in the Gulf of Alaska is related to the long seiche period of the shallow shelf.

5. The preferential radiation of energy toward the southeast is attributed to the orientation of the tectonic displacements along the continental shelf of the Gulf of Alaska.

6. The waves arriving at Cape Yakataga had their origin in the shallow coastal area near the Bering Glacier, whereas the waves arriving at Yakatat traveled through the deeper waters.

7. In Prince William Sound two major tsunamis were distinguished: one had its origin near the west coast of Montague Island, the other originated in the Port of Valdez.

8. Two types of tsunami-generating mechanisms were associated with the Alaska earthquake: (a) waves generated directly by tectonic movements of the sea floor, and (b) waves generated indirectly from landslides, mudflows, and slumping of alluvial deposits.

9. In Prince William Sound both generation mechanisms were evident, while in the generating area along the Gulf of Alaska, the generated tsunami was the direct result of tectonic movements.

ACKNOWLEDGMENTS
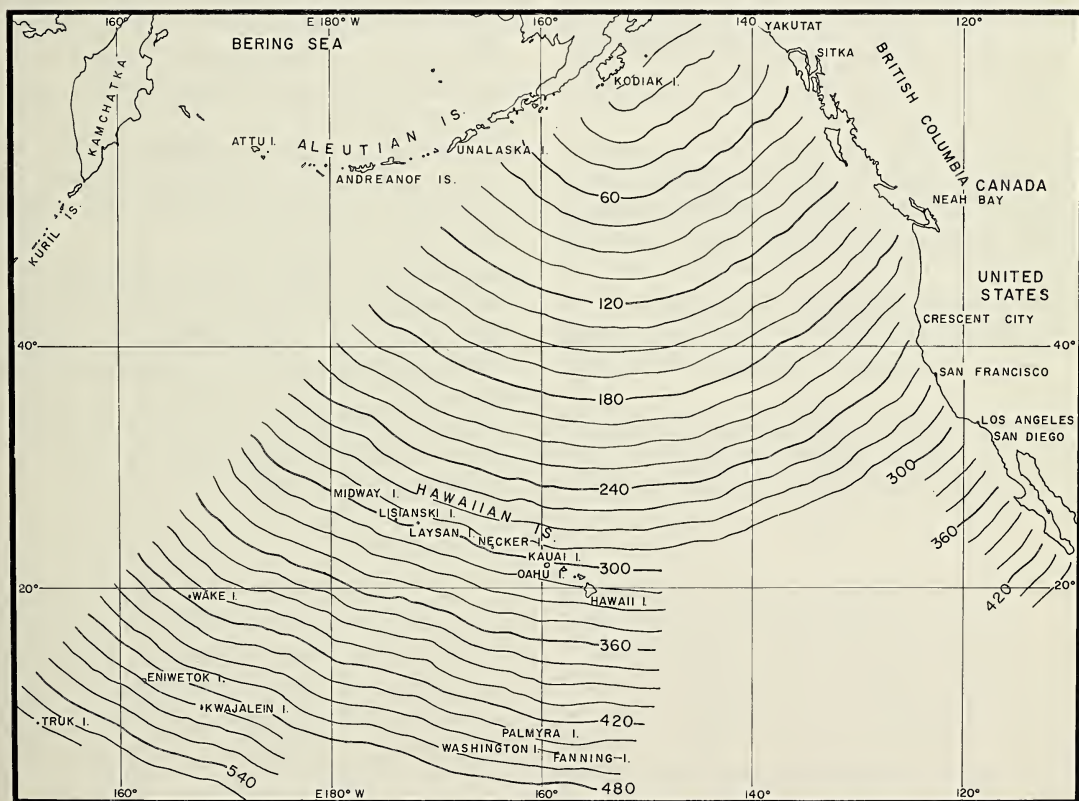
FIG. 6. Wave refraction diagram of the Alaska tsunami for the north Pacific Ocean (time interval: 15 minutes).

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A Study of the Source Mechanism of the Alaska Earthquake and Tsunami of March 27, 1964

Part II. Analysis of Rayleigh Wave[1]

Augustine S. Furumoto

ABSTRACT: The source mechanism of the Alaska earthquake of March 27, 1964 has been investigated by analyzing the Rayleigh wave recorded on the strain seismograph at Kipapa Station, Hawaii. The parameters that give the best fit to the observed data are: rupture length of 800 km, rupture velocity of 3 km/sec, and direction of rupture line of S30°W. The results of this analysis compare favorably with field data of elevation changes, with distribution of epicenters of aftershocks, and with the area of generation of the tsunami as obtained from sea-wave refraction diagrams.

THE UNITED STATES–JAPAN Cooperative Field Survey of the Alaska Earthquake of March 27, 1964 (Berg et al., in preparation) resulted in an estimate of the length and size of the rupture zone of the earthquake. Corroboration for these results was sought from seismic data. Toksöz et al. (1965) have published a source mechanism analysis using surface wave data. Their results are as follows: rupture velocity, 3.0 km/sec; rupture length, 600 km; azimuth of rupture, S50°W from the epicenter. These results, however, are at variance with the field survey data.

Shortly after the field survey, an attempt at source mechanism analysis by surface wave methods was made by using the record of the strain seismograph at Kipapa Station, Hawaii.

The results of this analysis are presented here because they are in somewhat better accord with field survey data.

This study was supported by funds from the National Science Foundation under Grants GP-2257 and GP-5111.

METHOD OF ANALYSIS

The analysis of source mechanism based on earthquake surface waves was developed by Ben-Menahem (1961). According to this method, if the Rayleigh wave is used the ratio of the amplitude spectrum of R_3 to the amplitude spectrum of R_2 can be related to directivity function $D(f)$,

$$D(f) = \frac{\left|\left(\frac{C}{V} + \cos\theta\right)\right] \sin\frac{\pi B f}{C}\left(\frac{C}{V} - \cos\theta\right)\right]\right|}{\left|\left(\frac{C}{V} - \cos\theta\right)\right] \sin\frac{\pi B f}{C}\left(\frac{C}{V} + \cos\theta\right)\right]\right|} \tag{1}$$

where C is the phase velocity of the curve at frequency f, V is the velocity of rupture propagation, B is the length of the rupture, and θ is the angle which the rupture line makes with the great circle path through the epicenter and observing station. A method using the Love

wave has also been developed, but the present study utilizes the Rayleigh wave only.

Ben-Menahem and Toksöz have applied the method of surface wave analysis to the study of the source mechanism for the Mongolian earthquake of 1958 (Ben-Menahem and Toksöz, 1962), the Alaska earthquake of 1958 (Ben-Menahem and Toksöz, 1963b), and the Kamchatka earthquake of 1952 (Ben-Menahem and

Toksöz, 1963*a*). Wada and Ono (1963) have applied the method for the Chile earthquake of 1960.

For the Alaska earthquake of 1964, copies of records from the strain seismograph at Kipapa Station, Hawaii, were used. This strain seismograph consists of a quartz rod 80 ft long. It was installed by the California Institute of Technology in the spring of 1963. Figure 1 shows the traces of R_2, R_3, and R_4.

RESULTS OF ANALYSIS

The Fourier spectra of R_2, R_3, and R_4 are given in Figure 2. To form the ratios of amplitudes R_3/R_2 and R_3/R_4, the decay of amplitudes with travel distance must be considered because the decay coefficient is frequency-dependent. The decay coefficient determined by Ben-Menahem and Toksöz (1963*a*) from empirical data was used for the corrections.

The amplitude ratios of R_3/R_2 and R_3/R_4 are given in Figure 3. There is coherence between the two ratio spectra at certain frequencies. Troughs of the spectra coincide at 0.0027 cps, 0.0056 cps, 0.0080 cps, and 0.0010 cps. Peaks agree at 0.0088 cps and 0.0111 cps. There is a peak at 0.0038 cps for R_3/R_4 and a peak

Fig. 2. *Upper*: Fourier spectrum of R_3. *Lower*: Fourier spectra of R_2 and R_4. The amplitude coordinate is in arbitrary units.

Fig. 1. *Upper*: Phases R_2 and G_3. Window indicates the section of R_2 that was used as data. *Middle*: Trace of R_3. *Lower*: Trace of R_4 and G_5.
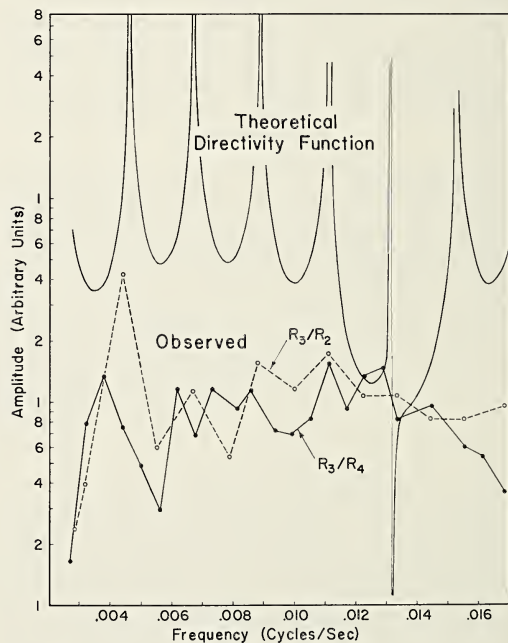
Fig. 3. Directivity function, theoretical and observed. The amplitude coordinate is in arbitrary units. For the theoretical curve, $V = 3$ km/sec, $\theta = 15°$, and $B = 800$ km.
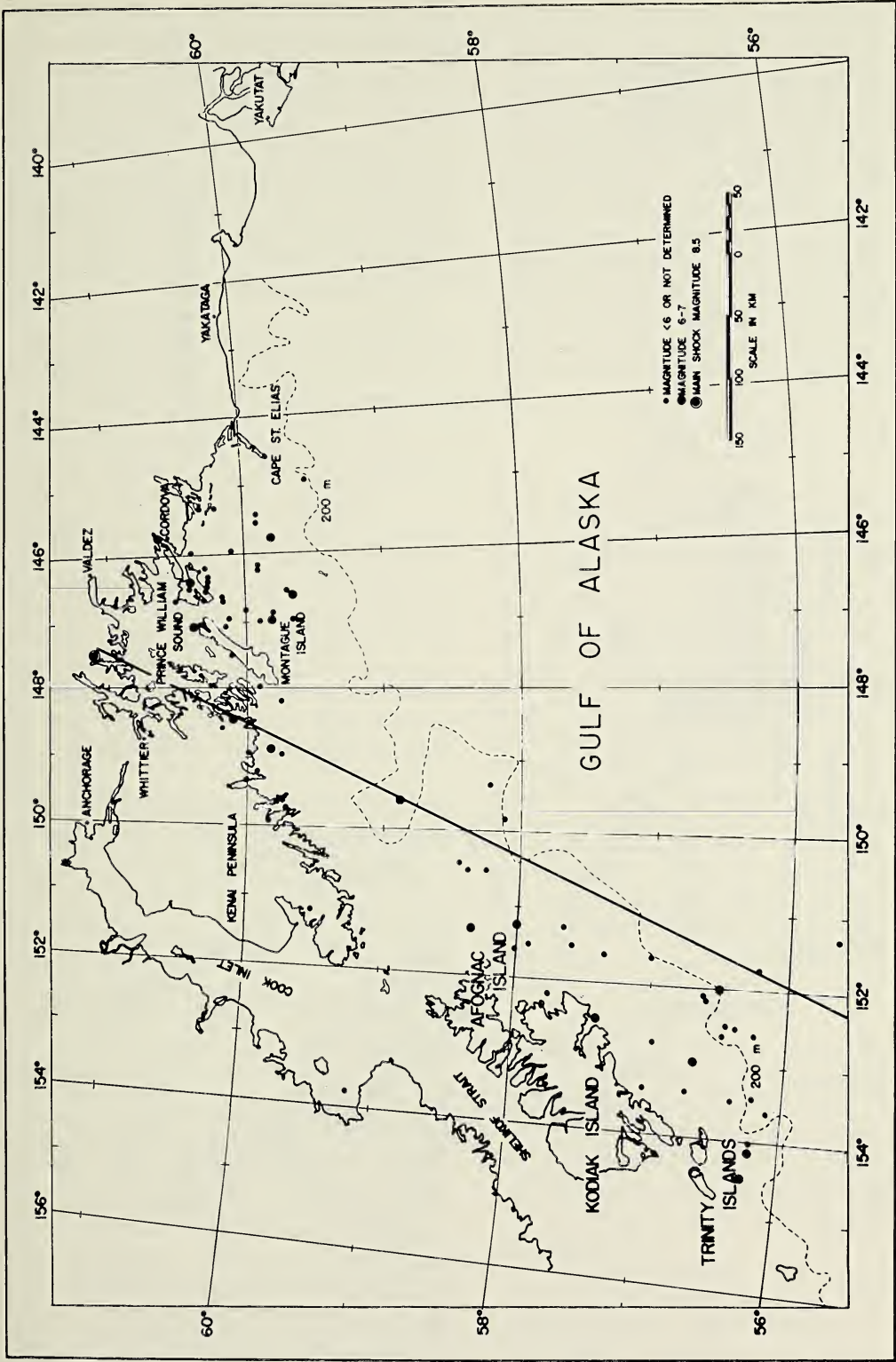
Fig. 4. The rupture line and distribution of epicenters of aftershocks.
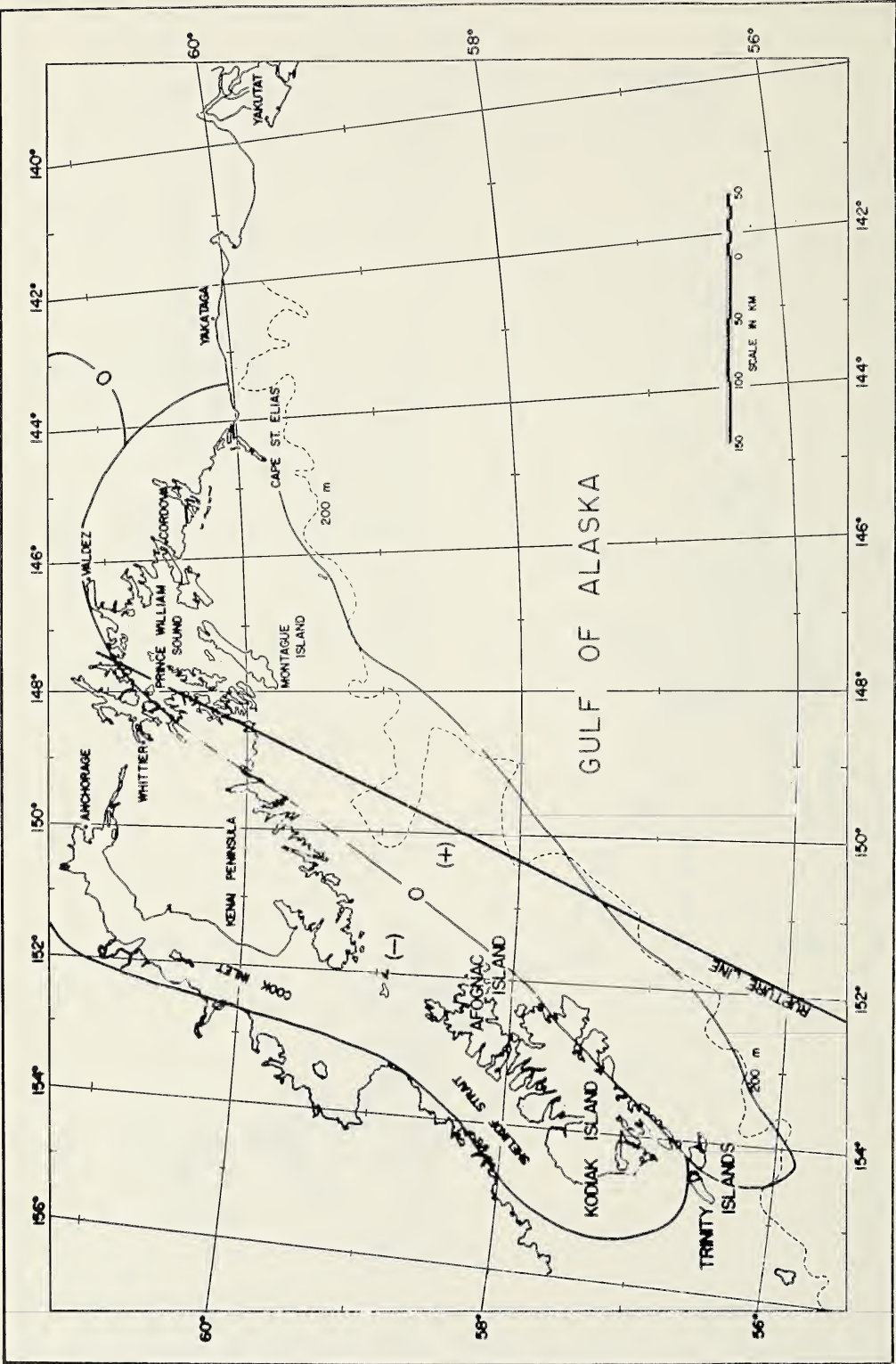
Fig. 5. The rupture line and elevation changes.

at 0.0044 cps for R_3/R_2. These two peaks probably coincide, and the apparent lag between the two is due to inadequate resolution of the Fourier analysis at these frequencies. There are opposing patterns at 0.0068 cps.

The best-fitting curve of the directivity function with the R_3/R_2 spectrum is plotted on the upper section of Figure 3. In this curve the parameters are: $B = 800$ km, $V = 3.0$ km/sec, and $\theta = 15°$. R_3/R_4 fits the curve also, except for the mismatch in the neighborhood of 0.0067 cps.

The epicenter determined by the U. S. Coast and Geodetic Survey (1964) was 61.05°N, 147.5°W. The coordinates of the Kipapa Station are 21°25′24″N and 158°00′54″W. The direction of the station from the epicenter is S15.3°W. This defines the direction of the rupture line from the epicenter as S30°W.

In Figure 4, the rupture line, as obtained from the present study, is superimposed on a map prepared by the U. S. Coast and Geodetic Survey (1964) which shows the epicenters of the main shock and the aftershocks of the Alaska earthquake. In general, the aftershock area defines the area of rupture. In the present case, the rupture line obtained from Rayleigh wave analysis extends 100 km beyond the aftershock area.

Surveys of elevation changes after the Alaska earthquake show positive changes in the Prince William Sound area, and negative changes in the Kodiak Island area. In Figure 5, the calculated line of rupture is superimposed on the map of elevation changes as prepared by Pararas-Carayannis (see his Fig. 1, on p. 302 of this issue). The rupture line runs diagonally across the section of positive changes. In this calculation the direction of the rupture line may vary about 5°. (This value is determined by the resolving power of the Fourier analysis.) If the direction of the rupture line is turned 5° clockwise, with the epicenter as the pivotal point, the rupture line will agree with the line of zero displacement from field observations.

An inspection of the directivity function $D(f)$ in equation (1) shows that the periodicity in terms of frequency of the peaks and troughs of the function is controlled by the length B of the rupture line. The peaks and troughs of R_3/R_2 and R_3/R_4 in Figure 3 are

such that a length of $B = 800$ km fits the data best. The superimposition of the rupture line on the elevation-change map shows that the rupture line extends to the south 100 km beyond the zone of elevation changes. On the other hand, if the total area of the observed elevation changes is considered, the zone has a length of 700–800 km (Plafker, 1965).

The present analysis shows a discrepancy between the direction of the calculated rupture line and the direction expected from field survey, but the discrepancy is within the limits of error of the calculation. The length of the calculated rupture line agrees with that from field data.

DISCUSSION

The results of the field survey by the United States–Japan Cooperative Team (Berg et al., in preparation) have heavily influenced the analysis presented here since the author was a member of the survey team. Perhaps because of this bias, the analysis should not be considered as an independent study but, rather, as additional evidence to strengthen the results proposed by the field survey. The rupture zone of the Alaska earthquake of 1964 has now been outlined consistently by four different methods: (a) field survey of elevation changes (Berg et al., in preparation; Plafker, 1965); (b) plot of epicenters of aftershock (U. S. Coast and Geodetic Survey, 1964); (c) tsunami refraction diagrams (Pararas-Carayannis, p. 301–310, in this issue); and (d) seismic surface wave method (this paper).

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Fungus Populations in Marine Waters and Coastal Sands of the Hawaiian, Line, and Phoenix Islands[1]

CAROL WRIGHT STEELE[2]

ABSTRACT: Saprophytic and facultative parasitic fungi present in the coastal waters and adjacent pelagic areas of the Hawaiian Islands, and in coastal sands of the Hawaiian, Line, and Phoenix islands, were isolated by plating methods. Isolates from all areas sampled indicate that abundant and varied fungus populations do exist in these environments. The number of fungi obtained from the inshore neritic zone was seven times that obtained from the oceanic zone. The fungus *Aureobasidium pullulans* (De Bary) Arnaud was isolated repeatedly from oceanic waters. A comparison is made between the genera and the average number of isolates per liter of water known from the Atlantic Ocean with those found in this study of the Pacific Ocean. The number of fungi isolated from sand samples of the different islands ranged from 2 to 1,600 per gram. Species diversity was evident throughout the samples. The leeward Hawaiian islands had a higher average number of isolates per gram than any other island group. In conclusion the problems of defining a marine fungus are discussed.

OCEANIC AREAS in different parts of the world have been shown to be habitats for marine fungi (Johnson and Sparrow, 1961). Investigators, however, have usually concentrated on particular groups of fungi by use of selective isolation methods (Barghoorn and Linder, 1944; Moore and Meyers, 1959; Jones, 1962). Only one extensive analysis of marine waters for a general fungus population is known, and it was made in the northwestern subtropical Atlantic Ocean (Roth et al., 1964). References to the occurrence of fungi in the Pacific Ocean are found (1) as incidental to studies of bacteria in marine water (ZoBell, 1946); (2) in studies of specialized fungi such as lignicolous fungi (Cribb and Cribb, 1955, 1956, 1960; Kohlmeyer, 1960; Meyers and Reynolds, 1960) and those on algae (Cribb and Cribb, 1955, 1956, 1960); and (3) in studies of particular kinds of fungi, e.g., Phycomycetes in Japanese waters (Kobayashi, 1953) and pathogenic species (Van Uden and Castelo Branco, 1961). Reports of fungi from terrestrial environments of islands in the central and southern Pacific

also are very limited. These include a few records of higher fungi collected in the Marshall Islands (Rogers, 1947), the Society Islands (Olive, 1957, 1958), and Raroia in the Tuamotu Archipelago (Cooke, 1961); Phycomycetes recovered by plating soils of the atolls of Bikini, Eniwetok, Rongerik, and Ronggelap (Sparrow, 1948); and Ascomycetes and Fungi Imperfecti from dung and soil samples collected by Olive in the Society Islands (Petersen, 1960). Consequently, as Cooke points out, the geographic distribution of fungi occurring on the islands of the Pacific is poorly known. Although studies have been initiated on the soils of the Hawaiian Islands (Baker, 1964) and the phyllosphere (Marsh, 1965), no study has been made of fungi occurring in marine waters and intertidal environments of these islands or elsewhere in the central Pacific. This investigation was undertaken to determine the occurrence and distribution of the saprophytic and facultative parasitic fungi which constitute the fungal populations of these habitats.

MATERIALS AND METHODS

Collection

Isolations for fungi were made from 59 water samples and 50 sand samples collected

from inshore areas of the Hawaiian Islands and adjacent pelagic environments. Seventeen sand samples were taken from the Phoenix and Line islands. The water samples were taken from four zones: the surf or spray zone; the inshore neritic zone, 2–200 m from shore; the offshore neritic zone, 300 m to 2 km from shore; and the oceanic zone, 2 km or more off shore. Of these water samples 56 were taken at the surface and 3 were taken at depths down to 600 m. The sand samples were taken from a depth of 2 inches in the supratidal, intertidal, and subtidal zones as delimited by Hedgpeth (1957). The sample sites were selected to include a variety of shore environments: leeward, windward, or areas of special interest (e.g., South Point, Hawaii, the southernmost point in the Hawaiian Islands; Waikiki Beach, probably the most frequently used beach on Oahu; and Midway Island, the northernmost inhabited island of the Hawaiian island chain.) Other samples were obtained as opportunity offered: those from Kure Island, the Phoenix Islands, the Line Islands, and the open ocean. Figure 1 gives the geographical location of the water and sand collection sites.

The surface water samples were collected in sterile 600-ml glass bottles with plastic screw caps. The closed bottles were immersed in the water, then opened and allowed to fill with water, closed underwater and brought to the surface. The depth samples were taken by sending a plastic water sampler of the van Dorn (1956) type to the designated depths. After the sampler was brought to the deck of the ship, a sterile 600-ml bottle was filled with water from the sampler.

All sand samples were collected with sterile implements and placed in sterile 100-ml jars with plastic screw caps or in sterile polyethylene bags (NASCO Whirl-Pak, Hydro Products Co., San Diego, California).

Salinity measurements were obtained by use of Quantabs SO51 (Linayer Corp., Detroit, Michigan). Temperature was determined by standard centigrade thermometer, and depth by standard oceanographic methods.

Isolation

Two principle means of isolation were employed: the pour-plate method (Salle, 1954)

and the millipore filter method (Roth et al., 1964).

Standard materials and procedures were used in the pour-plate method. Amounts plated for the water samples ranged from 0.5 ml to 5.0 ml. Dilutions of 1:10 to 1:100,000 were used for sand samples. Some samples were plated upon return to the laboratory; because of the distance between most sampling sites and the laboratory, however, most of the plating was done 24 to 48 hours after collection. All samples were kept under refrigeration until plated. A control plate, uninoculated, was set up for each medium for every plating. Plates were also exposed to the air during plating operations to determine the level of air contamination in the laboratory.

Materials for the millipore filter method included sterile cellulose-ester membranes with 0.45 μ porosity (Millipore Filter Corp., Bedford, Massachusetts). The samples were run through the millipore filter apparatus using a vacuum pump. The membranes with retained fungal elements were cultured on selective media in presterilized pastic petri dishes. The amount put through the filter ranged from 100 ml to 600 ml per sample. Controls were included for testing agar sterility and air contamination.

Several kinds of media were used: sodium caseinate agar (BBL 01-549, Fred and Waksman, 1928, modified by Potter, 1957), Roth's isolation medium (Roth et al., 1964), Fell's yeast agar (Fell et al., 1960) and mycobiotic agar (DIFCO 0689-02). All media except the mycobiotic agar were made with sea water collected at the sample sites. Bacterial growth was controlled by the incorporation of 0.05% chloramphenicol (Chloromycetin, Steri-Vial No. 65, Parke, Davis and Co.). Dilutions were made with McIlvaine's buffer solution, pH 7.0 (Machlis and Torrey, 1956). The mycobiotic agar was made with 250 ml sea water and 750 ml of distilled water in order to retain the selectivity of this medium in which chloromycetin is already incorporated.

The plates were placed in paper bags, sealed with adhesive tape, and incubated at 20°–24°C. Pour-plates were incubated for three weeks and the millipore filter plates for 10 days at room temperature (20°–24°C).
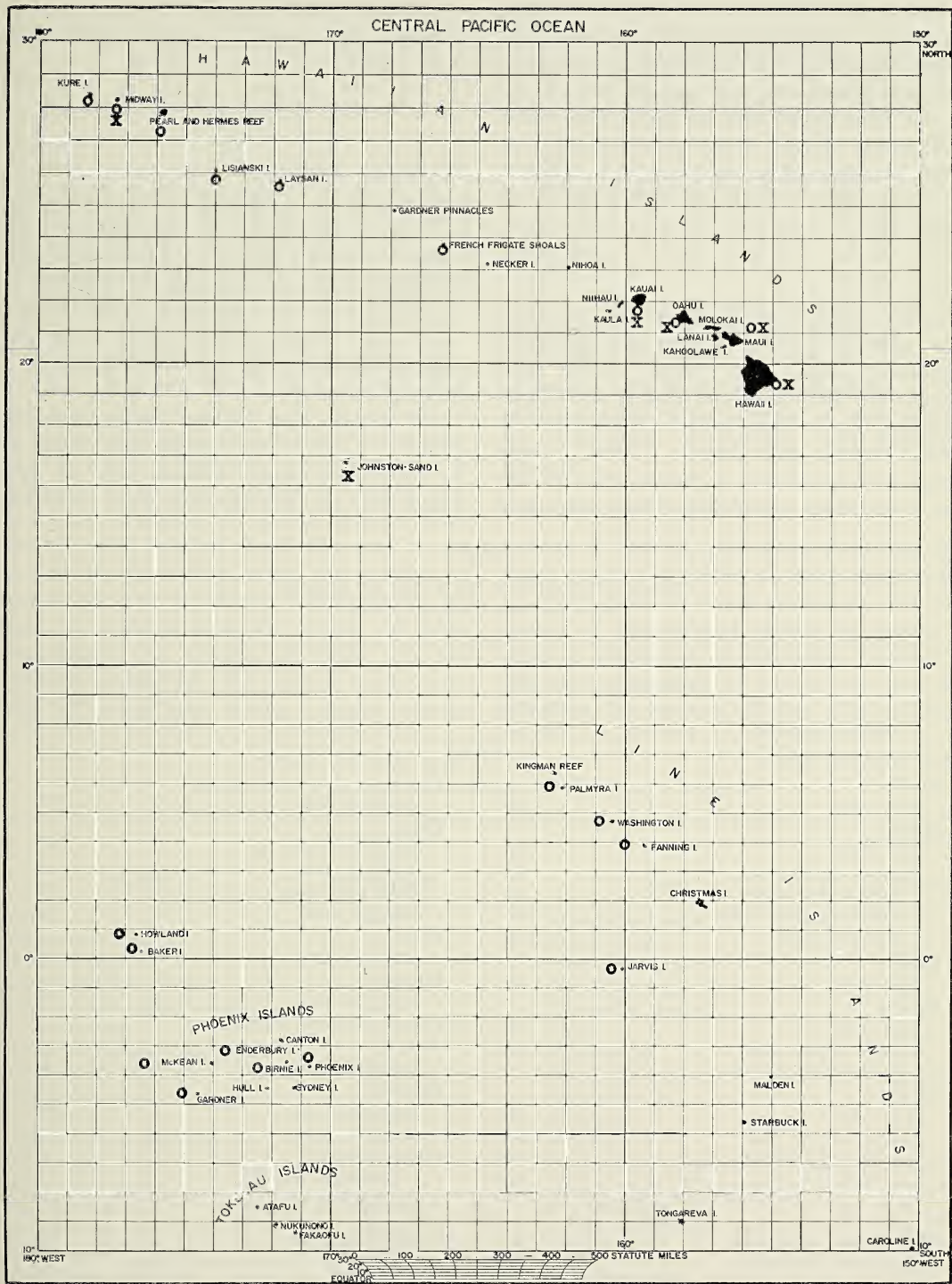
FIG. 1.   General geographical location of marine water and coastal sand collection sites. x, Marine water collection sites; o, coastal sand collection sites.

Other methods of isolation, such as baiting (Johnson and Sparrow, 1961), spread-plate technique (Buck and Cleverdon, 1960) and cellulose plates made by placing a piece of sterile filter paper over an agar plate before inoculating (Baker, 1964) were attempted on some samples. The pour-plate and millipore filter methods, however, proved superior for this study.

Identification

Some fungi were identified directly from the isolation plates by a technique employing pressure sensitive tape (clear acetate tape, Scotch No. 800, Minnesota Mining and Manufacturing Co.). This method is described by Roth, Orpurt, and Ahearn (1964). Other fungi were transferred to various selective media to encourage sporulation. Those used most

successfully were Czapek-Dox agar (DIFCO 0339-01) and "V-8" juice agar (Wickerham et al., 1946).

RESULTS

Populations in Water

Variations in salinity and temperature for all water sample sites was slight, ranging between 30 ‰ and 35 ‰ for salinity; between 20° and 25°C for temperature. Inasmuch as sampling was done over the period from June 1964 to May 1965 this temperature range also reflects the slight variation characteristic of a tropical climate.

All sample sites yielded fungus colonies (Table 1); 44 of the samples had counts of 50 colonies or under, whereas only 15 gave counts over 50. The standard plate count was

TABLE 1

Zonal Distribution of Fungi in Marine
Waters and Coastal Sands

WATER SAMPLES	NUMBER OF SAMPLES	AVERAGE NUMBER ISOLATES PER ML	SAND SAMPLES	NUMBER OF SAMPLES	AVERAGE NUMBER ISOLATES PER GM
Main Hawaiian islands			Main Hawaiian islands		
Kauai			Kauai		
Surf zone	2	.16	Intertidal zone	5	218
Oahu			Oahu		
Surf zone	9	.10	Supratidal zone	3	185
Inshore neritic zone	9	.83	Intertidal zone	3	6
Inshore bay zone	3	.28	Tidal pool zone	2	72
Offshore neritic zone	3	.61	Subtidal zone	3	14
Maui			Maui		
Surf zone	1	.17	Intertidal zone	1	36
Hawaii			Hawaii		
Surf zone	3	.09	Intertidal zone	6	77
Inshore neritic zone	5	.43	Leeward Hawaiian islands		
Leeward Hawaiian islands			Kure		
Midway			Intertidal zone	8	41
Surf zone	1	.20	Midway		
Inshore neritic zone	4	.031	Supratidal zone	1	1000
Oceanic, Johnston Island	9	.066	Intertidal zone	6	790
Oceanic, Oahu	7	.029	Other leeward Hawaiian islands		
			Intertidal zone	12	1220
Surf zone total	16	.12	Line Islands		
Inshore neritic zone total	18	.34	Intertidal zone	4	150
Inshore bay zone total	3	.28	Phoenix Islands		
Offshore neritic zone total	3	.61	Intertidal zone	13	80
Oceanic zone total	16	.045			
Polluted zone total	3	3.18			
GRAND TOTAL	59	.14	TOTAL	67	—

not significant for the dilutions used. There-fore, the number of isolates from the total number of milliliters used in plating is re-corded as an average isolation return per ml of water samples. The average number of iso-lates from any one sample ranged from 0.06 to 3.94 isolates per ml, with the average for samples at 0.14. The number of species ranged from 1 to 17 per sample. More than 50% of the sites, however, returned only 2 to 7 dif-ferent species (Steele, 1965). The predominant genera and species by percentage of occur-rence are listed in Table 2.

Table 3 lists the 126 species of fungi repre-senting 59 genera which were isolated from the water samples plated. The percentage of occurrence represents the number of water sam-ples in which a particular fungus occurred in reference to the total number of samples ana-lyzed. A tabulation of species isolated from the six zones sampled shows that they can be ranked in descending order for number of species per zone as follows: inshore neritic, 70; surf, 56; polluted zone, 28; oceanic, off John-ston Island, 23; oceanic, off Oahu, 20; and offshore neritic, 13. The inshore neritic zone was the richest area, having a higher average

number of isolates than either the surf or oceanic zones. A very low average number of isolates was obtained from both oceanic regions. The offshore oceanic area near Johnston Island returned more isolates than the comparable zone near Oahu, but both areas had about the same number of species. *Aureobasidium pullulans* and *Rhodotorula* spp. were common to both oceanic sites. These fungi were among those predominant in all isolations from water (Table 2).

As might be expected, samples from the polluted areas off Oahu had the highest aver-age number of fungi: 3.18 per ml. This was an area of diverse speciation. Members of the Sphaeropsidales were common, as were species of *Aspergillus, Penicillium,* and *Cephalo-sporium.*

Populations in Sand

From 67 sand samples plated from four dif-ferent zones, 134 species of fungi representing 71 genera were recovered (Table 3). The fre-quency of predominant isolates by species is given as percentage of occurrence (Table 2). The average number of isolates per gm, ob-tained by the standard dilution plate counting

TABLE 2

PREDOMINANT GENERA AND SPECIES IN WATER AND SAMPLES

WATER	PERCENTAGE* OF OCCURRENCE	SAND	PERCENTAGE OF OCCURRENCE
Yeasts	45.8	*Aspergillus wentii*	50.7
Rhodotorula spp.	27.1	*Fusarium* spp.	44.7
Fusarium spp.	22.0	*Phialophora* spp.	25.3
Cephalosporium curtipes	22.0	*Penicillium* spp.	22.3
Cladosporium cladosporioides	16.9	*Aspergillus niger*	20.8
C. epiphyllum	16.9	Yeasts	20.8
Helminthosporium anomalum	16.9	*Megaster* sp.	17.6
Trichoderma lignorum	15.2	*Masoniella grisea*	16.4
Aspergillus niger	13.5	*Aspergillus* spp.	14.9
A. wentii	13.5	*A. terreus*	13.4
Aureobasidium pullulans	13.5	*A. ustus*	11.9
Phoma spp.	11.8	*Trichoderma lignorum*	11.9
Aspergillus spp.	11.8	*Cladosporium cladosporioides*	11.9
Black yeasts	11.8	*C. epiphyllum*	11.9
Pestalotia spp.	10.1	*Cephalosporium roseo-griseum*	11.9
Cladosporium herbarum	10.1	*C.* spp.	11.9
Aspergillus versicolor	10.1	*C. acremonium*	10.4
Penicillium spp.	10.1	*C. curtipes*	10.4
		Penicillium lilacinum	10.4

* The percentage of occurrence represents the number of water or sand samples in which a particular fungus occurred in reference to the total of 59 water samples or 67 sand samples analyzed (Orpurt, 1964).

TABLE 3

GENERA AND SPECIES ISOLATED FROM MARINE WATERS AND COASTAL SANDS

NAME	PERCENTAGE OCCURRENCE IN WATER SAMPLES	PERCENTAGE OCCURRENCE IN SAND SAMPLES
PHYCOMYCETES		
Mucorales		
Cunninghamella echinulata Thaxter		1.4
C. sp.		1.4
Mucor globosus Fischer		1.4
Rhizopus nigricans Ehrenberg	1.6	2.9
Syncephalastrum racemosum (Cohn) Schroeter	1.6	1.4
ASCOMYCETES		
Chaetomium olivaceum Cooke and Ellis		1.4
C. sp.	1.6	
Melanomma sp.		1.4
Melanospora lagenaria (Pers.) Fuckel		1.4
M. sp.		1.4
Microascus intermedius Emmons and Dodge		1.4
M. trigonosporus Emmons and Dodge		1.4
Neurospora sp.	5.0	2.9
Sporormia sp.		2.9
BASIDIOMYCETES		
Sp. indet.	1.6	
DEUTEROMYCETES		
Sphaeropsidales		
Amerosporium sp.		1.4
Aposphaeria sp.	5.0*	
Coniothyrium fuckelii Sacc.	1.6	
Cytosporina sp.	3.3	
Diplodia sp.		1.4
Diplodina sp.	1.6	
Macrophoma sp.	1.6	
Peyronellaea sp.	3.3	
Phoma hibernica Grimes	3.3	2.9
Phoma spp.	11.8	7.1†
Phomopsis sp.	1.6	
Phyllosticta sp.	1.6	
Piggotia sp.	1.6	
Pyrenochaeta sp.	1.6	1.4†
Sphaeronaema spinella Kalchb.	1.6	
Sporonema sp.		1.4
Melanconiales		
Pestalotia sp.	10.1	5.9†
Phylactaena sp.	1.6	
Moniliales		
Sporobolomycetaceae		
Sporobolomyces sp.		2.9‡
Moniliaceae		
Acremonium sp.		1.4‡
Acrostalagmus cinnabarinus Corda	1.6	1.4
Aleurisma carnis (Brooks and Hansford) Bisby		1.4†
Allescheriella crocea (Mont.) Hughes	1.6	
Aspergillus amstelodami (Mangin) Thom		1.4‡

TABLE 3 (*continued*)

NAME	PERCENTAGE OCCURRENCE IN WATER SAMPLES	PERCENTAGE OCCURRENCE IN SAND SAMPLES
A. caespitosus Raper and Thom		1.4
A. candidus Link		4.4‡
A. carneus (van Tiegh) Bloch.		4.4‡
A. clavatus Desm.		2.9‡
A. effusus Tiraboschi		1.4‡
A. flavipes (Bainier and Sartory) Thom and Church	3.3	2.9
A. flavus Link	1.6*	1.4
A. fumigatus Fres.	1.6	4.4‡
A. granulosus Raper and Thom		7.1
A. itaconicus Kinoshita	1.6*	
A. janus Raper and Thom	1.6	4.4
A. luchuensis Inui	1.6	2.9
A. micro-virido-citrinus Cost. and Lucet	1.6	
A. nidulans (Eidam) Wint.		1.4
A. niger van Tiegh.	13.5*	20.8‡
A. niveus Bloch.		1.4
A. ochraceus Wilhelm	3.3	
A. oryzae (Ahlburg) Cohn	1.6	2.9
A. panamensis Raper and Thom		2.9
A. proliferans G. Smith	1.6*	
A. restrictus G. Smith		1.4
A. ruber (Spieckermann and Bremer) Thom and Church		1.4
A. sulphureus (Fres.) Thom and Church	3.3	1.4
A. sydowi (Bain. and Sart.) Thom and Church	3.3*	7.1‡
A. tamarii Kita	1.6*	2.9‡
A. terreus Thom	3.3	13.4‡
A. unguis (Emile-Weil and Gaudin) Thom and Raper		1.4‡
A. ustus (Bainier) Thom and Church	1.6	11.9‡
A. versicolor (Vuill.) Tiraboschi	10.1*	5.9‡
A. wentii Wehmer	13.5*	50.7†‡
A. spp.	11.8*	14.9
Botryophialophora marina Linder		2.9
Cephalosporium acremonium Corda	3.3*	10.4†‡
C. asperum Marchal		1.4
C. coremioides Raillo		1.4
C. curtipes Sacc.	22.0*	10.4
C. humicola Oudemans	3.3*	1.4
C. roseo-griseum Saksena	6.7*	11.9‡
C. sp.	1.6	11.9
Fusidium viride Grove	1.6	1.4
Gliocladium fimbriatum Gilman and Abbott		1.4
Malbranchea sp.		1.4
Moeszia sp.	1.6	
Monilia brunnea Gilman and Abbott		1.4
Monocillium sp.	1.6	5.9‡
Paecilomyces fusisporus Saksena	1.6*	
P. varioti Bainier	1.6	2.9
Penicillium albidum Sopp		1.4
P. brevi-campactum Dierckx	3.3	
P. canescens Sopp	3.3	
P. caseicolum Bainier	1.6	1.4
P. charlesii Smith	1.6	1.4‡

TABLE 3 (*continued*)

NAME	PERCENTAGE OCCURRENCE IN WATER SAMPLES	PERCENTAGE OCCURRENCE IN SAND SAMPLES
P. chermesinum Biourge		1.4
P. citrinum Thom	1.6	8.9‡
P. commune Thom	1.6	
P. corylophilum Dierckx		1.4‡
P. cyaneo-fulvum Biourge	1.6	
P. cyaneum (Bainier and Sartory) Biourge	1.6	
P. janthinellum Biourge	3.3	
P. kapuscinskii Zaleski		1.4‡
P. lanosum Westling	6.7	1.4
P. lanoso-coeruleum Thom	5.0	
P. lilacinum Thom	6.7*	10.4
P. miczynskii Zaleski		1.4
P. nigricans (Bainier) Thom	8.4	8.9‡
P. notatum Westling	5.0	
P. oxalicum Currie and Thom	1.6	1.4
P. piscarium Westling		1.4
P. purpurrescens Sopp	1.6	
P. raciborskii Zaleski	1.6	
P. rotundum Raper and Fennell		1.4‡
P. simplicissimum (Oud.) Thom	1.6*	
P. steckii Zaleski	1.6	4.4‡
P. velutinum van Beyma		2.9
P. spp.	10.1*	22.3†‡
Rhinotrichum sp.		1.4†‡
Scopulariopsis brevicaulis Bainier		4.4‡
S. brumptii Salvanet-Duval		1.4‡
S. carbonaria Morton and G. Smith	1.6	
S. croci van Beyma		1.4‡
S. fimicola (Cost. and Mat.) Vuill.	1.6	2.9
S. sp.	1.6	7.1
Sepedonium sp.	1.6	2.9
Spicaria simplicissima Oudemans	1.6*	
Sporotrichum epigaeum Brunard		2.9
Trichoderma album Preuss	3.3	
T. glaucum Abbott	1.6	2.9
T. koningi Oudemans	5.0*	1.4
T. lignorum (Tode) Harz	15.2*	11.9
Trinacrium sp.		1.4
Tritirachium album Limber		1.4
T. purpureum (Saito) Beyma	3.3*	
Varicosporium sp.		1.4
Verticillium candelabrum Bonorden	1.6	
V. terrestre (Link) Lindau	3.3	1.4
Dematiaceae		
Acrostaphylus sp.		1.4
Acrotheca sp.		1.4
Alternaria fasciculata Cooke and Ellis	1.6	1.4‡
A. geophila Daszewska	1.6	
A. humicola Oudemans	3.3	
A. tenuis Nees	3.3	
Aureobasidium mansonii (Cast.) Cooke		1.4‡
A. pullulans (De Bary) Arnaud	13.5*	8.9†‡
A. sp.	1.6	4.4‡

TABLE 3 (*continued*)

NAME	PERCENTAGE OCCURRENCE IN WATER SAMPLES	PERCENTAGE OCCURRENCE IN SAND SAMPLES
Bispora sp.		1.4
Catenularia sp.	1.6	
Chalaropsis sp.	1.6	
Chloridium sp.	1.6	
Cladosporium cladosporioides (Fres.) de Vries	16.9*	11.9†‡
C. epiphyllum Persoon	16.9*	11.9
C. herbarum (Persoon) Link	10.1	8.9†‡
C. lignicolum Corda	3.3	
C. spp.		10.4
Cordana sp.		2.9†
Curvularia geniculata (Tracy and Earle) Boedijn	6.7	1.4‡
C. interseminata (Berkeley and Ravenel) Gilman	3.3	
C. pallescens Boedijn	3.3	4.4
C. subulata (Nees) Boedijn	3.3*	
C. tetramera (McKinney) Boedijn	3.3	
Dendryphion sp.	1.6	
Gliobotrys alboviridis von Hohnel		1.4
Gliomastix convoluta (Harz) Mason		8.9
Gonytrichum macrocladum (Sacc.) Hughes	1.6	
G. sp.		1.4
Hansfordia togoensis Hughes	1.6	
H. sp.	1.6	
Helminthosporium anomalum Gilman and Abbott	16.9	1.4
H. sativum Pammel, King and Bakke	1.6	
Heterosporium sp.		1.4
Hormodendrum cladosporioides (Fresenius) Sacc.	1.6	
Humicola grisea Tragen	1.6	
H. lanuginosa (Griff and Maubl.) Bunce		1.4
H. nigrescens Omvik		1.4
H. sp.		2.9
Macrosporium cladosporioides Desm.	1.6	
M. sacrinaeforme Cavara	1.6	
Masoniella grisea (Smith) Smith	5.0	16.4‡
Megaster sp.		17.6†‡
Menispora apicalis Berk. and Curt.	1.6	
Nigrospora sphaerica (Sacc.) Mason	3.3	8.9†
Oidiodendron citrinum		1.4
O. griseum Robak.		1.4
Passalora sp.		1.4
Periconia byssoides Persoon		1.4
P. hispidula (Pers. ex Pers.) Mason and M. B. Ellis		1.4
Phialophora sp.	8.4	25.3†‡
Scolecotrichum sp.		1.4†
Stachybotrys atra Corda		1.4
S. lobulata Berkeley		4.4
Stemphylium botryosom Wallrath	1.6	
S. macrosporoideum (Berkeley and Broome) Sacc.	3.3	
Torula allii (Harz) Sacc.	1.6	
T. lucifuga Oudemans		4.4‡
T. sp.		1.4‡
Trichocladium sp.		1.4
Zygosporium masonii Hughes		4.4
Stilbaceae		

TABLE 3 (*continued*)

NAME	PERCENTAGE OCCURRENCE IN WATER SAMPLES	PERCENTAGE OCCURRENCE IN SAND SAMPLES
Didymostilbe sp.	1.6	
Graphium sp.		1.4
Harpographium sp.	1.6	
Synnematium jonesii Speare	3.3	1.4
Tuberculariaceae		
Cylindrocarpon didymum (Hartung) Wollenweber		2.9†
C. radicicola Wollenweber		1.4
Epicoccum purpurascens Ehrenb.	1.6	
E. sp.		2.9
Fusarium merismoides Corda	1.6	
F. spp.	22.0*	44.7†‡
Hymenella sp.		4.4†
Myrothecium roridum Tode	3.3	
M. verrucaria (Alb. and Schw.) Ditmar ex Fr.	·	1.4
M. sp.	1.6	1.4
Yeasts		
Rhodotorula spp.	27.1*	1.4
Orange yeasts	1.6	8.9†‡
Pink yeasts		2.9†
Black and orange yeasts		1.4
Black yeasts	11.8*	8.9†‡
Yeasts	45.8*	20.8†‡
Mycelia sterilia (Dematiaceae)	28.8*	37.3†‡
Mycelia sterilia (Moniliaceae)	16.9*	40.1†‡

* Isolated from oceanic zone.
† Isolated from the Line Islands.
‡ Isolated from the Phoenix Islands.

technique, is given in Table 1. A total of 37 samples had fewer than 100 isolates per sample; the remaining 30 samples had more than 100 isolates per sample. The sand of the leeward Hawaiian islands had the highest number of isolates, over 500 per sample, but the number of different species was lower than in comparable samples from the Phoenix Islands.

The sands returned from 1 to 35 species per sample. The majority yielded from 3 to 9 species each. The intertidal sands of the main Hawaiian islands returned the highest number of species, a total of 68. Black Sand Beach, Hawaii, and Kaena Point, Oahu, each yielded totals of 16 species. The supratidal zone of Kuhio Beach, Oahu had the highest number of species for sites in that zone: 35 species among 16 genera. The zone total was 53 species. The subtidal zone returned the lowest number of species, only 22.

In Table 2, the 18 fungi occurring most frequently in water and sand are listed. Among these, 9 are common to both areas although of different rank for percentage of occurrence; 7 occur in water and not sand, and 8 occur in sand, not in water. Of those common to both water and sand, yeasts, aspergilli, and penicillia were common to all sand samples. Neither *Rhodotorula* spp. which is penultimate in rank for water, nor *Aureobasidium pullulans,* also frequent in water samples, was predominant for sand samples.

The control plates poured when both water and sand samples were plated showed no growth. Only one colony was observed on a plate exposed to determine the level of air contamination in the laboratory.

DISCUSSION

Isolates obtained from water samples indicate that abundant and varied fungus popula-

tions do exist in this environment, but that frequencies vary with zones. The oceanic zone had fewer isolates than did the other zones studied in the pelagic region. This result was expected, inasmuch as oceanic regions are known to have lower populations of marine organisms than do regions closer to land. Of the 59 water samples, 50 were taken from areas that are strongly influenced by the presence of oceanic islands, whereas the other 9 were from areas well away from any shore. Areas near islands are known to support abundant and varied marine life. Ships may also be a source of water pollution, and therefore modified populations might be expected in shipping lanes.

Differences can also be observed between the two oceanic locations studied, as reflected in differences in kind of fungi present but not in numbers. The oceanic area off Johnston Island contained more yeasts than did surface samples obtained near the island of Oahu. The latter had more fungi which would be classified as terrestrial, such as aspergilli and penicillia. The high yeast population observed from the oceanic areas is in agreement with the findings of both ZoBell (1946) and of Fell and Van Uden (1963). Members of the genus *Rhodotorula* were isolated consistently from all water samples, including the depth samples. Roth et al. (1962) have noted the common occurrence of these yeasts in oceanic localities, an observation now confirmed by these studies for the Pacific Ocean.

When the three zones—surf, inshore neritic, and offshore neritic—are compared, a correlation is found between numbers of isolates per ml and location of zone. This is not unexpected. This correlation is particularly clear in the data for these zones in Oahu. The surf zone, which is an unstable area with constant wave action, returned 0.10 isolates per ml compared with 0.33 for offshore neritic and 0.83 for inshore neritic zones. Species of *Curvularia, Alternaria,* and *Helminthosporium* were isolated repeatedly from the inshore neritic zone. This zone, in the area of Oahu, is richer in number of species than is the same zone on Hawaii. This might be due to pollution, as Oahu has a greater population and has a major port for shipping. Members of the order

Sphaeropsidales, of the Fungi Imperfecti, were frequently found in the Oahu samples. These fungi are parasitic on plants. The polluted area contained much floating debris which could serve as a source of these fungi.

Some water samples were taken from tidal pools in the intertidal zone. In every case there was a high number of isolates. Intertidal pool populations may be affected by higher temperatures, higher organic content, salinity levels, or wave action. One area, however, that of a large bay on the windward side of Oahu, did not return a high yield of isolates. This area has a high fresh-water run-off which reduces the salinity at the surface as much as 5 ‰ during the rainy season. Even though the area had a lower population than expected, it did have great diversity, explained perhaps by the run-off factor. The high number of aspergilli and penicillia isolated was to be expected because of their proclivity for sporulation, cosmopolitan habitat, and their great adaptability. A good percentage of these might be run-off and/or air contaminants introduced into the water.

The fact that more fungi were isolated from the sand than from the water supports the well-known observation that microbial populations are higher in relation to fixed surfaces. Examination of Table 3 also shows that the general population of sand is quite different than that of water.

The high number of isolates from the sand samples taken from the leeward Hawaiian islands and the few species among them is in direct contrast with the low number of isolates and high number of species in the samples from the Phoenix Islands and the Line Islands. There could be many reasons for this. The elapsed time before plating the leeward samples was greater than for those of the Phoenix and Line islands. Variations in bird population, temperature, and humidity, and shore stability among the leeward Hawaiian islands, may be critical factors controlling fungus populations. If the bird population serves as a control, a survey for keratinophilic and coprophilous species might be rewarding. Such a survey should also extend to other islands with large bird populations. Another factor influencing fungus populations, as reflected in the high number

of species returned from the Phoenix and Line islands, is the fact that Gardner Island, Washington Island, and Palmyra Island are, or have been, inhabited.

The supratidal zone gave the highest average number of isolates per gm. This zone is a very stable area, a mixture of soil and sand. When the average number of isolates is compared for the supratidal, intertidal, and subtidal zones on Oahu, the intertidal displays the lowest average number of isolates, which may be explained by the influence of constant washing by the waves. The tidal pool area of the sand, like the tidal pool area of the water, is characterized by the presence of more fungi than are found in the surrounding areas of each zone.

Two of the sand areas sampled are unique among sands for their color and composition, namely a green sand beach and a black sand beach. The black sand beach had 259 isolates distributed through 12 genera and 200 species, while the green sand beach had 28 isolates, in 10 genera and 12 species. Although 4 genera were common to both, only 1 species, *Aspergillus terreus,* occurred at both sites. Both beaches are on the island of Hawaii. One reason for this difference may be that the black sand beach is continually exposed to contamination from people and their litter, while the green sand beach is in a very remote location. Another reason could be the difference in the chemical composition of the sands. Black sand is formed from basalt lava rock and cinders, and green sand is formed by the release of olivine crystals which are in the basalt lava rock.

Most of the Phycomycetes and the Ascomycetes were isolated from sand. These fungi are known to adhere to substrates. Only one species predominates over the others, *Aspergillus wentii,* as shown in Table 2. When plating four samples on mycobiotic agar from beaches that are local tourist attractions on Oahu, one potential pathogen was found: *Microascus intermedius,* which has been isolated from a number of soils by mouse passage. Several species of this genus are known to be etiologic agents of dermatophytoses and onychomycosis in man (Barron et al., 1961).

It is interesting to compare the results obtained by Roth et al. (1964) in the Atlantic with the results obtained from this study in the Pacific. Roth took 227 water samples and identified 41 genera among his isolates. This study encompassed 59 water samples and resulted in the identification of 59 genera. Of these, 29 genera were common to both lists. The Atlantic list included 11 genera not reported in this study; this study includes 29 genera not reported by Roth et al. (1964).

Table 4 shows the difference in average number of isolates per liter between the samples taken in the Atlantic Ocean and those taken in the Pacific Ocean.

Furthermore, it is a striking fact that no Pacific sample, either water or sand, was without fungi, whereas Roth et al. (1964) recovered fungi from only 80% of their 227 samples. Because they did not include sand samples in their study, comparisons can be made only between water samples. The maximum number of

TABLE 4

COMPARISON OF NUMBERS OF ISOLATES FROM THE ATLANTIC OCEAN AND THE PACIFIC OCEAN

ATLANTIC OCEAN (ROTH ET AL. 1964)			PACIFIC OCEAN (1965)		
DEPTH	NUMBER OF SAMPLES	AVERAGE NUMBER ISOLATES PER LITER	DEPTH	NUMBER OF SAMPLES	AVERAGE NUMBER ISOLATES PER LITER
500 to	5	11.1	600 m	1	13.0
1000 m	17	12.1	300 m	1	6.0
	9	4.9	300 m	1	10.0
	2	1.0			
Surface	12	15.5	Surface	1	18.0
to	79	17.5		1	55.0
500 m	43	15.1		1	30.0
	16	3.0		1	73.0

species per offshore sample in the Atlantic was 6. In the Pacific the number ranged from 1 to 11. Although the maximum number of species per Pacific sample exceeds that reported for the Atlantic, the total number of species found in each area is approximately the same: 133 species in the Atlantic compared with 127 in the Pacific. The diversity of genera is notably higher in the Pacific samples. Samples from both areas yielded fungi that were not identified.

There are both differences and similarities between the kinds of fungi obtained from the two regions. A total of 30 species were common to Atlantic and Pacific waters. Neither Ascomycetes nor Basidiomycetes were reported for the Atlantic. From the Pacific water 2 Ascomycetes and 1 Basidiomycete were recovered. Roth et al noted the low incidence of Phycomycetes, reporting only 6. Five species were identified in this Pacific study, but only 2 were from water samples. Species of Sphaeropsidales occurred in similar numbers in both oceans: 7 in the Atlantic and 5 in the Pacific, but only 2 species were common to both. In comparing the species of fungi which are predominant in each area, some species are found on both lists. Roth et al. distinguished 8 fungi each from the eulittoral and oceanic water samples as their dominant species. Of these, *Aureobasidium pullulans* was most common in the oceanic zone and it did not occur in their eulittoral list. In the Pacific, this fungus was common in water but ranked seventh among 18 species. *Cladosporium* species (*sic*) were the most common fungi in the Atlantic eulittoral samples, and occupied second place in the oceanic list. Two species, *Cladosporium cladosporioides* and *C. epiphyllum,* ranked high among those frequent in both water and sand samples of the Pacific. *Trichoderma lignorum,* the last species on the Atlantic list of eulittoral dominants, is absent from the corresponding oceanic list. In the Pacific it occurred in both water and sand samples, although much more frequently in water than in sand. In summary, the differences suggest that the Pacific fungus population is different from that of the Atlantic.

Having established the fact that fungi can be isolated from Pacific as well as Atlantic water and shores, there still remains the problem of how one determines whether or not a certain isolate is a marine fungus. There is no single diagnostic test. The criteria which have been suggested are summarized by Roth et al. (1964) and may be stated as: (1) the isolate must grow and reproduce exclusively or predominantly in the sea or on intertidal substrata, or (2) the isolate must grow and reproduce at an optimal level in the normal salinity of the oceans. None of these criteria can be supported without qualification. There is still no means of concrete demonstration of growth and reproduction of a fungus in vivo in marine environments except for those fungi growing on natural (and introduced) substrata. If growth and reproduction at normal salinity levels is accepted as a criterion, this allows for the inclusion of fungi found in salt lakes (Anastasiou, 1963). Moreover, Gray (1963) has shown that many fungi of terrestrial origin are capable of better growth in sea water media than in fresh water media. If growth is limited to natural substrata, then the possibility of free-living marine fungi is excluded.

As more investigations of marine habitats are undertaken, the number of genera and species isolated from them will undoubtedly increase. Many of the genera found in the Pacific are known from other marine locations, e.g., species of *Aureobasidium, Macrophoma, Phoma, Diplodina, Diplodia, Epicoccum, Fusidium, Cladosporium, Alternaria,* and *Macrosporium* (Johnson and Sparrow, 1961). Repeated isolation, however, is not confirmatory evidence, but is only suggestive. Roth et al. (1964) contend that, until further distributional and physiological data are obtained, fungi so isolated should be regarded as of incidental occurrence in the sea. Nor is the rare isolation of a species from only marine habitats reliable evidence, as this may reflect only the randomness of the sampling and the samplers. Curiously, *Dendryphiella arenaria* Nicot., which is dominant in Atlantic eulittoral samples and known only from marine sources, was not among the Pacific isolates. Conversely, *Botryophialophora marina,* also known only from marine sources, was found in the Pacific but not in the Atlantic.

In conclusion, a working definition for a marine fungus is proposed: A marine fungus is one which is capable of producing successive generations by sexual and/or asexual means in

natural oceanic waters or on intertidal substrata. Until experimental means of proof are devised, the data presented here will serve as contributory evidence for the distribution of fungi isolated from marine habitats.

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Distribution and Movements of Birds in the Bering and Chukchi Seas

L. G. SWARTZ[1]

THIS PAPER reports on pelagic observations of about 29 species of birds in the northern Bering Sea and the Chukchi Sea during a cruise in the late summer of 1960. This work represents part of a larger study of the sea bird colonies at Cape Thompson, Alaska (Swartz, 1966).

The problems presented by the offshore distribution and movements of sea birds have proved refractory to many workers. Primarily, efforts to delineate and solve these problems have been incidental to other objectives of sea voyages and have centered in the North Atlantic and Barents Sea. Wynne-Edwards (1935) has brought together much of this scattered work from the North Atlantic, and Belopolski (1957) summarized data from the Barents Sea. Recently, Kuroda (1960) and Shuntov (1961) have published observations extending into the Bering Sea. Jacques (1930) is the only worker to publish substantial pelagic observations north of Bering Strait.

THE ENVIRONMENT

An intensive investigation of the Chukchi Sea (Fig. 1) began in 1959 when the Department of Oceanography of the University of Washington, under the direction of Dr. R. H. Fleming, and the Bureau of Commercial Fisheries sent their respective research vessels, the "Brown Bear" and the "John Cobb," to the area. These organizations together undertook extensive physical, chemical, and biological investigations. In 1960, the Department of Oceanography sent the "Brown Bear" to these waters again in order to extend and verify the results of the 1959 cruise.

Two publications (Wolfe, 1960, 1962) include brief summaries of the scope of the marine programs but present little actual data.

The results of these projects have been presented in preliminary form in several reports prepared for the individual financing agencies. Formal publication has been made of some of the University of Washington work (Creager and McManus, 1961; Fleming et al., 1961; Fleming and Heggarty, 1962), and a large volume has recently been published including the work of many individuals which provides comprehensive coverage of almost all aspects of the marine environment included within the scope of this paper (see Swartz, 1966).

The following brief summary of the characteristics of this environment is summarized from personal experience, the preliminary reports mentioned, the published works, and from personal communication and conversation with the individuals involved in the marine programs.

The Chukchi Sea, in which most of the
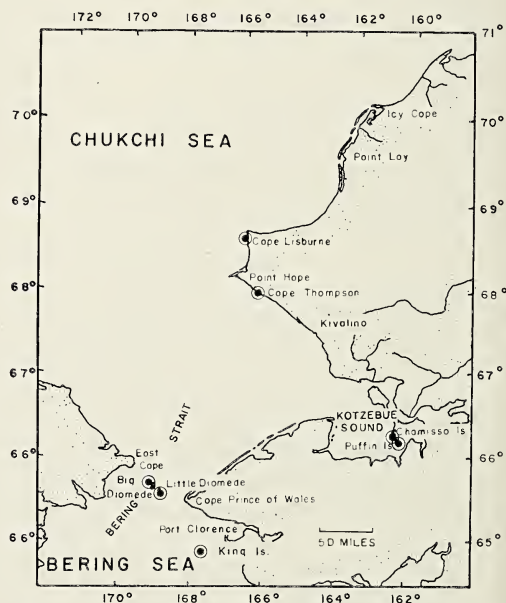
FIG. 1. The Bering and Chukchi seas showing the area included within this study. Major sea bird colonies near the cruise track are indicated with the circular symbol.

pelagic bird observations were made, is shallow with a relatively featureless bottom (Fig. 2). In the area sampled, few depths exceed 35 fathoms. Current and temperature patterns are complex. In general, current flow is northward through Bering Strait (Fig. 4). Patterns of current flow in the northern Chukchi Sea seem to be affected strongly by winds. Temperature patterns at 5-m depths are shown in Figure 5. The invertebrate fauna is rich and abundant, but fishes are not conspicuously abundant in either species or individuals, though of course their numbers are adequate to support sea bird colonies in apparent prosperity (Swartz, 1966).

PROCEDURE

The portion of the cruise track of the "Brown Bear" which is included in this paper is shown in Figure 3. Willoughby boarded the "Brown Bear" on August 6 near Cape Thompson and disembarked at Nome on August 28.

Most observations were made from the flying bridge where the view in all directions was relatively unobstructed. In order to achieve an objective index of abundance and movements, 10-minute-long counts of all birds seen and records of their activities were made at intervals throughout the 24-hour period. Detailed observations were continued between the 10-minute counts to the extent permitted by weather, visibility, and the endurance of the observer. Over 600 entries pertaining to sea birds were made in addition to 10-minute counts. Latitude and longitude are known for each entry. Observations including time, position, surface temperature of the sea, wind speed and direction, wet and dry bulb air temperature, barometer readings, precipitation, size and direction of swell, and approximate visibility were recorded several times a day from routine readings made by Willoughby and other ship personnel. All of these data were examined and those which proved meaningful in interpreting the avian observations are discussed at the appropriate place. Since conditions of visibility varied widely from day to day, no effort was made to convert the data to absolute abundance per square unit of sea surface as was done by Kuroda (1960).

During the same interval that Willoughby was making observations at sea, a shore party was conducting investigations of the large colonies at Cape Thompson. It was hoped that comparisons of behavior at the breeding cliffs with offshore observations would yield significant information not otherwise obtainable. With the exception of the expected observation that departure of flocks from the cliffs produced a rise in numbers observed at sea, this hope was not realized.

RESULTS

Below, listed phylogenetically, are discussions of distribution, abundance, and movements of birds seen from the "Brown Bear." Unless specifically noted, all species were previously observed in the Bering or Chukchi seas by Jacques (1930) or Shuntov (1961), the only authors who have published substantial offshore observations which overlap those reported here.

Loons (Gavia sp.)

Two sightings of unidentified loons were made, both close to shore (Fig. 6). Four of these birds were seen at 69°46'N, 163°17'W
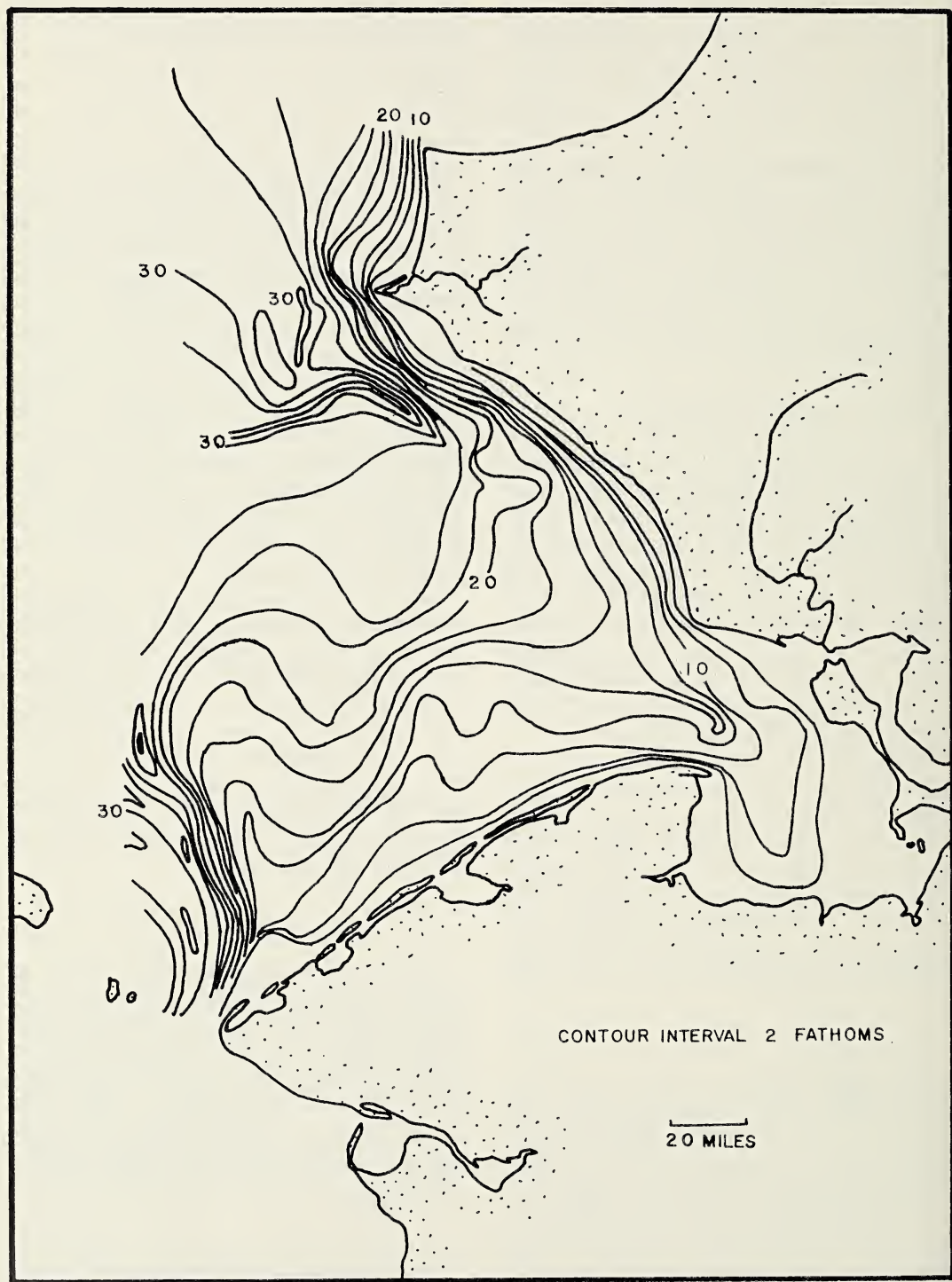
FIG. 2. The Bering and Chukchi sea showing bottom contours. (Modified from Creager and McManus, 1961.)
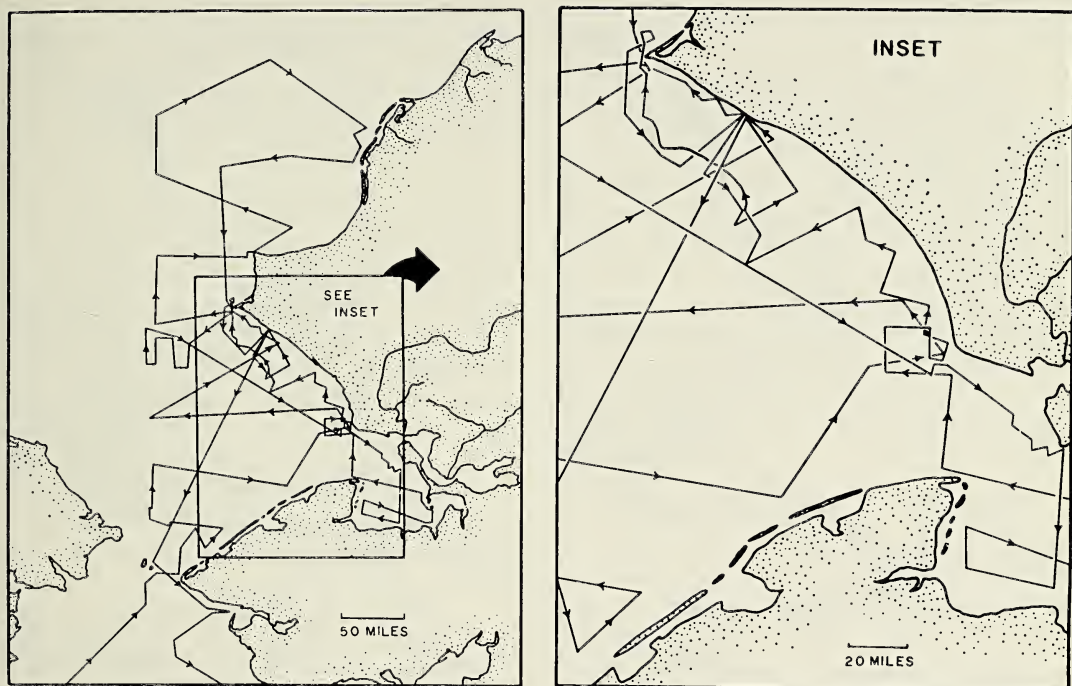
FIG. 3. The Bering and Chukchi seas, showing the portion of the cruise track of the "Brown Bear" included within this study. (Modified from Fleming et al., 1960.)

between Point Lay and Icy Cape; another was seen near Chamisso Island in Kotzebue Sound.

Fulmar (Fulmarus glacialis)

Fulmars were seen on 11 occasions (Fig. 6), ordinarily as single birds. Two birds were seen together near Bering Strait and three or four near Little Diomede Island amid a large number of alcids. Feeding concentrations as seen by Kuroda (1960:59) were not observed but, on the other hand, Fulmars were not abundant during any part of this voyage. Shuntov (1961: 1063) described Fulmars as the most abundant bird in the Bering Sea west of the Pribilofs. Jacques (1930:360–361) remarked on their abundance near the Pribilofs and off East Cape but, in common with observations from the "Brown Bear," he saw them only occasionally in the Chukchi Sea. All the Fulmars observed (14 or 15) were the light phase, which agrees with the observations of Jacques (1930:361) that in the Arctic the light phase greatly predominates.

Shearwaters

Probably all shearwaters seen (Fig. 7) were Slender-billed Shearwaters (*Puffinus tenuiros-*

tris), but they could not always be identified with certainty. It is possible that some were Sooty Shearwaters, though no records are known from north of the Aleutian Islands (Gabrielson and Lincoln, 1959:80–81). The former species, which breeds in the southern hemisphere, spends its nonbreeding season in northern waters and has been collected and observed as far north as Point Barrow (Gabrielson and Lincoln, 1959:78). Several of the sightings reported here were feeding flocks, on one occasion near Cape Thompson comprising between 500 and 1,000 individuals. In no case, however, did abundance approach the concentrations that have been observed by other authors south of Bering Strait (see Gabrielson and Lincoln, 1959:79; Shuntov, 1961:1061–1062).

Cormorants (Phalacrocorax)

Cormorants were identified on four occasions (Fig. 7), chiefly within sight of nesting cliffs. One doubtful sighting was made near Chamisso Island in Kotzebue Sound. Cormorants were presumably all Pelagic Cormorants (*P. pelagicus*), but doubt exists in some cases. An observation about 20 miles from Little Diomede
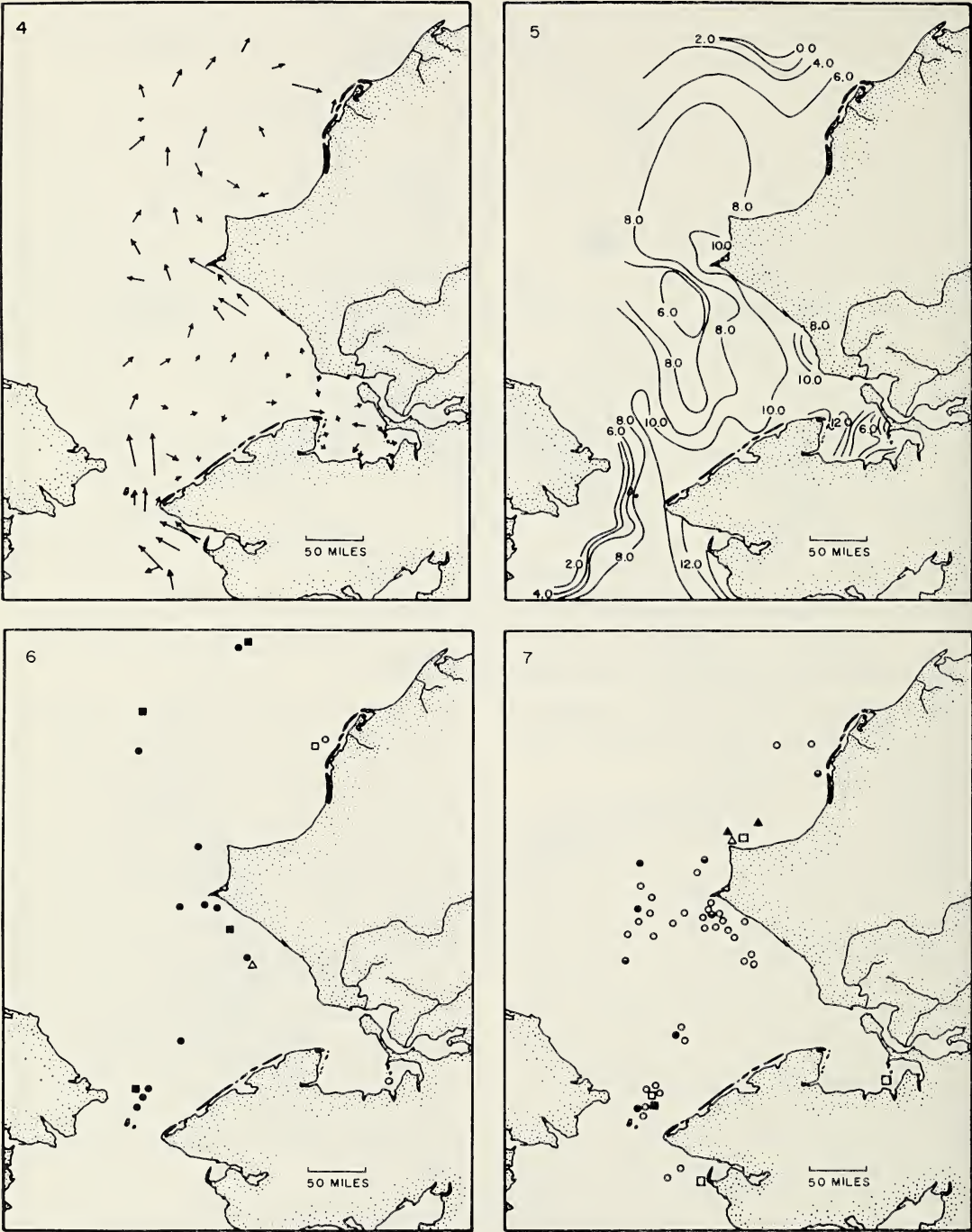
FIG. 4. Surface currents (5.0 m). Vector length indicates speed of current. (From Fleming and Heggarty, 1960.)

FIG. 5. Surface (5.0 m) isotherms. (From Fleming et al., 1960.)

FIG. 6. Observations of loons, ○; the Fulmar, ●; Pectoral Sandpiper, □; unidentified sandpipers, ■; and the Long-billed Dowitcher, △.

FIG. 7. Observations of the Slender-billed Shearwater, ○; unidentified shearwaters, ●; cormorants, □; the Old Squaw, ■; Common Eider, △; Spectacled Eider, ▲; and unidentified eiders, ◐.

Island represents the maximum distance these birds were seen from shore or nesting colonies. Jacques (1930:362) apparently did not observe cormorants north of Bering Strait, but his voyage did not bring him close to breeding colonies so this is not surprising.

Old Squaw (Clangula hyemalis)

Numerous Old Squaws were seen very close to shore between Cape Thompson and Point Hope by the shore party, but only a single pelagic observation (near Bering Strait) was made (Fig. 7). This pattern of distribution is probably typical of this species during the breeding season.

Common Eider (Somateria mollissima)

One sighting was made of 19 Common Eiders close to the shore of Cape Lisburne (Fig. 7).

Spectacled Eider (Lampronetta fischeri)

Two sightings were made, one single individual and one flock of four, both near the Cape Lisburne cliffs (Fig. 7).

Unidentified Eiders

Four sightings of small flocks of unidentified eiders were made, only one more than a few miles offshore (Fig. 7).

Pectoral Sandpiper (Erolia melanotos)

This species was identified only at one location, off Point Lay (Fig. 6), when a single bird landed on the deck of the "Brown Bear" and walked about for 5 minutes. A Pectoral Sandpiper was seen flying 15 minutes later and may have been the same bird. Jacques (1930:353–366) did not observe this species. Shuntov (1961:1066) observed sandpipers in the Bering Sea, but did not identify the species.

Unidentified Sandpipers

Sandpipers which could not definitely be identified were seen on four occasions (Fig. 6), two of which were more than 100 miles from shore.

Long-billed Dowitcher
(Limnodromus scolopaceus) (?)

A single individual, probably of this species,

was observed about 30 miles off the coast near Kivalina (Fig. 6).

Red Phalarope (Phalaropus fulicarius)

All identified phalaropes were of this species, but it is possible that some Northern Phalaropes (*Lobipes lobatus*) were present in the area. Jacques (1930:364) commented to similar effect that probably all the phalaropes he saw in the Arctic Ocean were Red Phalaropes. Red Phalaropes were seen at 28 locations, mostly in groups of 3–6, although 13 solitary individuals were seen. Observations were widely scattered over the course of the cruise, but none were made south of Bering Strait (Fig. 8).

Unidentified Phalaropes

In many cases, it was not possible definitely to identify phalaropes. No doubt most, if not all, of the unidentified birds were Red Phalaropes (Fig. 8).

Pomarine Jaeger (Stercorarius pomarinus)

Seven scattered sightings of this species were made, all north of 67°N (Fig. 9). Four of these were single birds, two sightings were of two birds, and one of "several." Jacques (1930:357) found it to be common or abundant north of Bering Strait during about the same time of year. Shuntov (1961:1065) observed a northerly movement of Pomarine, Parasitic, and Long-tailed Jaegers in the southern Bering Sea in the end of May and beginning of June, which probably represented migration to breeding grounds. He saw Pomarine Jaegers commonly, but only infrequently observed the other species.

Parasitic Jaeger (S. parasiticus)

This species was seen on 12 occasions (Fig. 9). As was the case with the previous species, all sightings were made north of 67°N. Eight sightings were of single individuals, one of three, two of two, and one of "several."

Long-tailed Jaeger (S. longicaudus)

This species, though far more abundant as a breeding bird at least in the Cape Thompson area than the two preceding species, was almost entirely absent in the pelagic observations. Only two birds were seen (Fig. 9).

Fig. 8.   Observations of the Red Phalarope, ○; and unidentified phalaropes, ●.
Fig. 9.   Observations of the Pomarine Jaeger, ○; Parasitic Jaeger, ●; Long-tailed Jaeger, △; and un-
identified jaegers, ▲.
Fig. 10.   Observations of the Sabine's Gull, ○; Arctic Tern, ●; Yellow Wagtail, △; and the Water
Pipit, ▲.
Fig. 11.   Abundance, distribution, and movements of the Pigeon Guillemot, ○; Kittlitz's Murrelet, ●; Para-
keet Auklet, □; Crested Auklet, ■; Least Auklet, △; unidentified auklet, ▲; Horned Puffin, ◓; and Tufted
Puffin, ◖. Numbers and direction of flight in both species of puffins is indicated by size of symbol and
direction of vector: o, 1–5; ○, "some"; ◯, hundreds. C indicates the birds were circling.
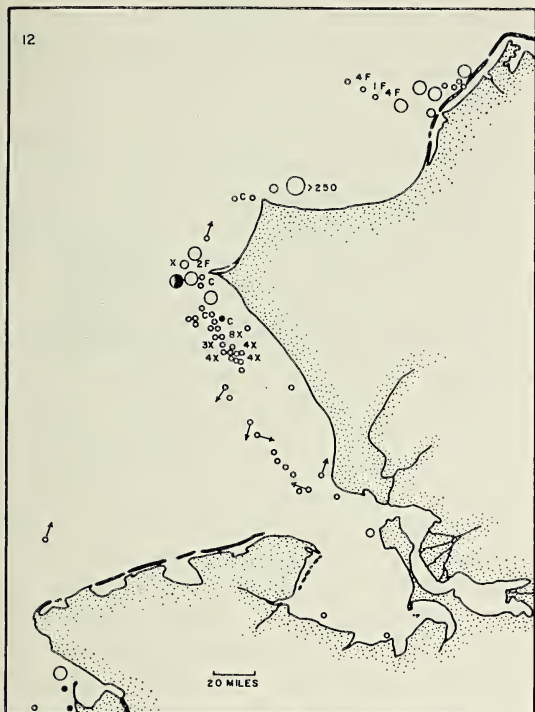
Fig. 12. Abundance, distribution, and movements of Glaucous Gulls (*open* and *half open circles*) and Herring Gulls (*black circles*). Numbers and direction of flight of Glaucous Gulls indicated by size of symbols and direction of vectors; smallest circle, 1–5; ○, 6–10; ◯, 11–20; ◖, 21–40; ◯, more than 150. C indicates circling, F indicates following the ship, and X indicates birds on the water.

Fig. 13. Abundance, distribution, and movements of Black-legged Kittiwakes. Numbers and direction of flight are indicated by size of symbols and length and direction of vectors: smaller circle, 1–5; ○, 11–20; shortest arrow, 1–5; → 6–10; ⟶ 11–20; C indicates circling and X indicates birds on the water.

Unidentified Jaeger

Jaegers were seen but could not be identified on 15 occasions. These observations were widely scattered but all were north of 67°N (Fig. 9).

Glaucous Gull (Larus hyperboreus)

Adult and immature Glaucous Gulls were most abundant at the cliffs and beaches where they fed extensively on the eggs and chicks of other species, especially murres. They were seen frequently to about 25 miles offshore and only occasionally at greater distances (Figs. 12 and 14). This species and, to a lesser extent, kittiwakes often followed the ship for up to several hours at a time. Both species fed on garbage thrown overboard. Although some tendency to fly into the wind was observed from shore and from the ship, no large movements of Glaucous Gulls in response to wind

were evident. Such movements by larids have been observed by other authors, however (e.g., Harrison, 1955:109–110).

Herring Gull (Larus argentatus)

Two doubtful sightings of immature birds (possibly the same bird sighted at different hours) were made 16–18 miles west northwest of Cape Thompson on August 24. Groups of two, four, and three individuals were sighted near shore in the vicinity of Port Clarence (Fig. 12). All Herring Gulls sighted were immature.

Black-legged Kittiwake (Rissa tridactyla)

Both adult and immature kittiwakes were common on the open ocean (Fig. 13). Adults were often in winter plumage. The adults in breeding plumage and immatures were most abundant near the nesting cliffs, but the radius of their daily movements from the cliffs is not

clearly demonstrated (Fig. 15). It seems likely that breeding kittiwakes do not regularly fly out to sea as far as murres, but rather feed closer to shore. Regular patterns of movements which may exist are not evident from the data. Kittiwakes do not exhibit as distinct a pattern of daily activity fluctuations as do murres (Swartz, 1966), and do not characteristically fly as straight a course, so that possible flight trends might tend to be obscured. No movement, abundance, or distributional phenomena associated with daily rhythms are evident.

One kittiwake in winter plumage was collected at about 70°50′N, 165°30′W near the edge of the polar ice pack. The reproductive tract was undeveloped and brood patches were not present. It is likely that many of the adult kittiwakes seen on the open ocean far from shore are nonbreeders.

Sabine's Gull (Xema sabini)

These birds were seen on six occasions and all but one were immatures (Fig. 10). The only adults (six birds) were seen at 70°46′N, 165°42′W, near the northernmost point on the cruise track. No particular distributional pattern is evident.

Arctic Tern (Sterna paradisaea)

Arctic Terns were seen on 11 occasions in groups of from 1 to 17 birds, of which 7 were immature and the rest (43) were adults. Most of the sightings were within about 50 miles of a shoreline and all but 1 were within 40 miles of land (Fig. 10).

Murres (Uria lomvia and U. aalge)

Thick-billed and Common Murres are very similar in appearance and could not be differentiated consistently under the conditions prevailing at sea. They are therefore considered together and such differences as exist between them are discussed at the appropriate places.

The abundance and distribution of murres is plotted in Figures 16, 17, and 18. Due to the large total number of observations, only ten-minute count data are presented. Murres were the most abundant birds on the Chukchi Sea and were almost always visible from the ship even far from shore. Murres were seen in all but 24 (16%) of the 146 ten-minute

counts. Of these 24 negative counts 19 were made in an area near and within Kotzebue Sound in which very few birds of any kind were seen.

Clear correlations between murre distribution and water temperature were found in this study. A striking decrease in the number of murres was noted on August 14 as the ship passed from colder waters to the warmer waters near Kotzebue Sound, crossing the 9°, 10°, 11°, and 12°C isotherms as plotted by Fleming et al. (1960: Fig. 5). (These isotherms represent the temperature 5 meters below the surface.) R. H. Fleming (personal communication) has observed this correlation on previous cruises in the area. Storer (1952:185) showed that the main breeding range of the Thick-billed Murre lies in areas where the August surface water temperatures are below 10°C and that the temperature tolerance of the Common Murre tends to be somewhat higher. Storer (1952:187) cited Salomonsen's (1944) claim that low temperatures retard spring molt and breeding in murres. This is clearly a local or individual response and would reinforce the contention that water temperatures could in part account for local distribution patterns.

As the ship passed deeper into Kotzebue Sound on August 14 a subsequent sharp drop in water temperature occurred, but no increase in murres was evident except near Chamisso and Puffin islands, where small numbers of Common Murres were seen. Grinnell (1900:7) reported "immense numbers" of Thick-billed Murres breeding on these islands but did not report Common Murres. Neither species seems any longer to be an abundant breeder.

The situation with regard to distribution and temperature is complex and at present remains unclear. Possibly not only water temperature but salinity, food supply, depth, and distance from breeding concentrations are interrelated factors. The speculation that a progressive northern range extension of the Common Murre is occurring which is correlated with long-term warming trends is provocative. Far too few data are available at present, however, to consider the hypothesis in detail.

In colder waters, murres were seen on all but 3% of the 10-minute counts. Even in these cases, murres were observed between the count-

100+   14
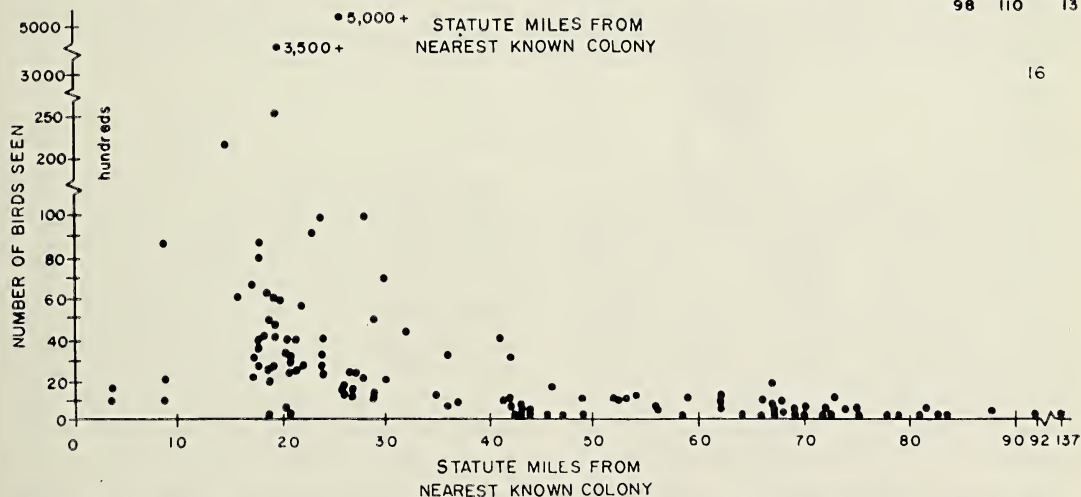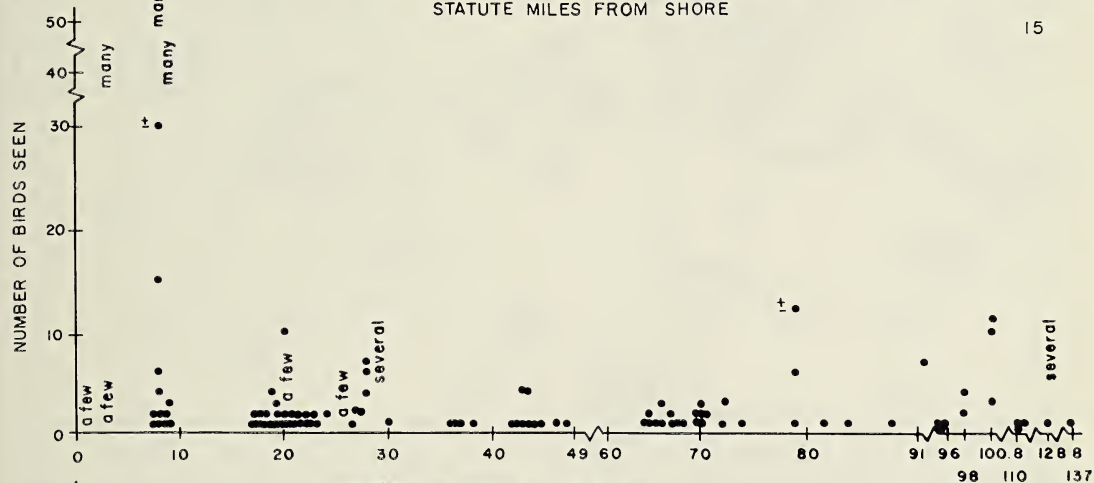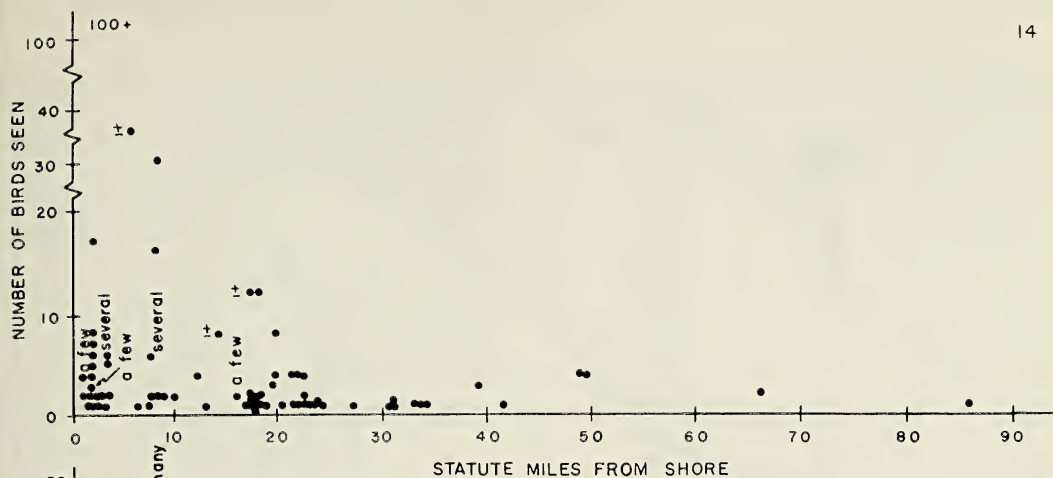
FIG. 14. Abundance of Glaucous Gulls vs. distance from the nearest shore. Since Glaucous Gulls may nest at many points along the shore, comparison is made between abundance and distance from the nearest land. All entries are included.

FIG. 15. Abundance of Black-legged Kittiwakes vs. distance from the nearest known colony. Because of incomplete knowledge of nesting colonies, observations from 10-minute counts near and in Kotzebue Sound are not included. All other observations are plotted.

FIG. 16. Abundance of murres vs. distance from the nearest known colony. Due to the great amount of data available, only 10-minute counts are plotted. Because of incomplete knowledge of nesting colonies, data from 10-minute counts in and near Kotzebue Sound are omitted.

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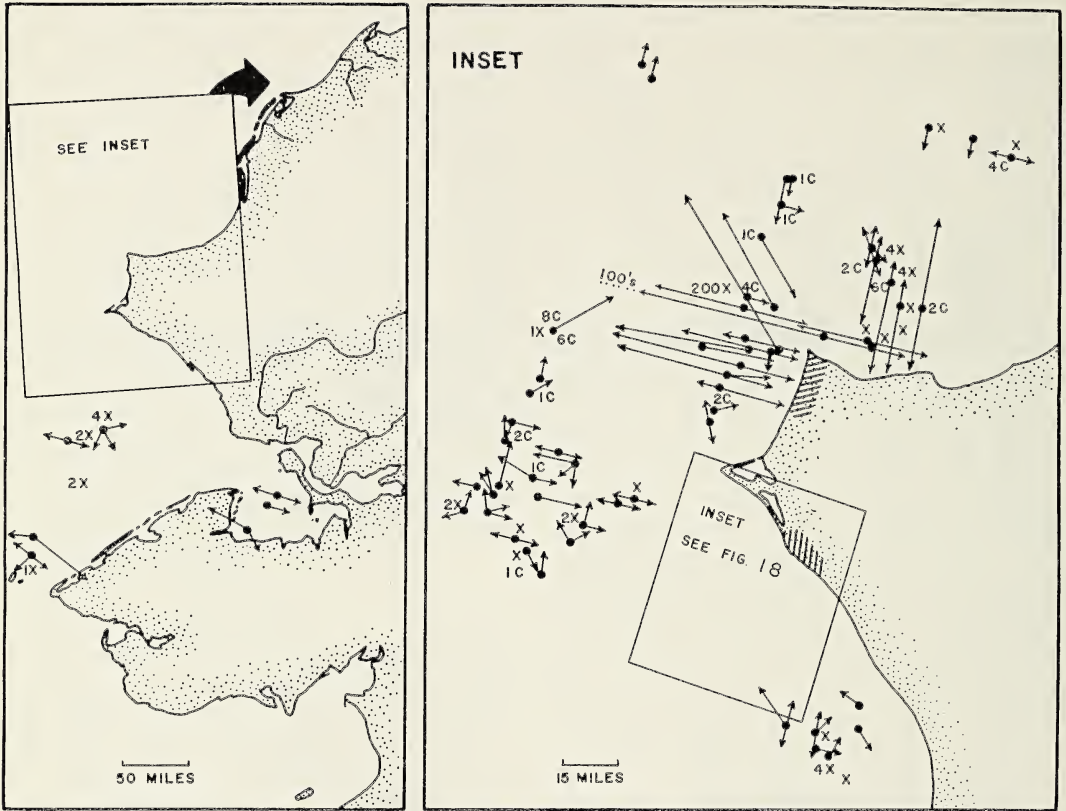
Fig. 17. Abundance, distribution, and movements of murres (10-minute counts only). Abundance is indicated by length of vector and, when not in flight, by numbers at the point of observation. The number is printed on the vector when more than 100. *C* indicates circling; *X* indicates that the birds were on the water. Cape Lisburne (*top*) and Cape Thompson colonies are indicated by *cross hatching*.

1–5	→
6–10	⟶
11–20	⟶

| 21–30 | ⟶ |
| 31–50 | ⟶ |

| 51–80 | ⟶ |
| 81–100 | ⟶ |
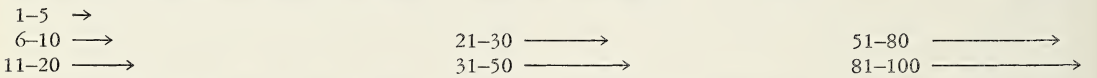
ing intervals. Although distinguishing the two species was difficult unless the birds came very close to the ship, it appears that away from the colonies at Cape Thompson and Cape Lisburne (in general, 5 miles offshore and beyond), Thick-billed Murres greatly outnumber the Common Murres, probably making up more than 90% of the murre population on the open ocean. On the nesting cliffs, the population is believed to include 60% Thick-billed Murres (Swartz, 1966), implying that Common Murres prefer shallower water than do thick-bills. This is consistent with data on food habits (Swartz, 1966), which imply that Common Murres feed in shallower water. The area on the open ocean in which the fewest murres were seen was near the ice pack at about 70°50′N, 166°00′W.

The greatest number of murres was found within about 40 statute miles from the nearest colony (Fig. 16). It is apparent from Figures 16, 17, and 18 and from direct observation of feeding activities made from the ship that the usual feeding activity of breeding birds takes place within about 40 miles of the nesting cliffs and mostly within about 30 miles. Since murres are strong flyers and are capable of flying at least 50 mph (Vaughan, 1937:123; Baxter and Rintoul, 1953; Portaz, 1928; Frohawk, 1928, in: Tuck, 1960:23), a feeding distance of 30–40 miles seems reasonable. Feeding areas for the Cape Thompson colonies seem to be primarily south of Point Hope, and those for the Cape Lisburne colonies north and west of the Cape Lisburne cliffs, although some over-
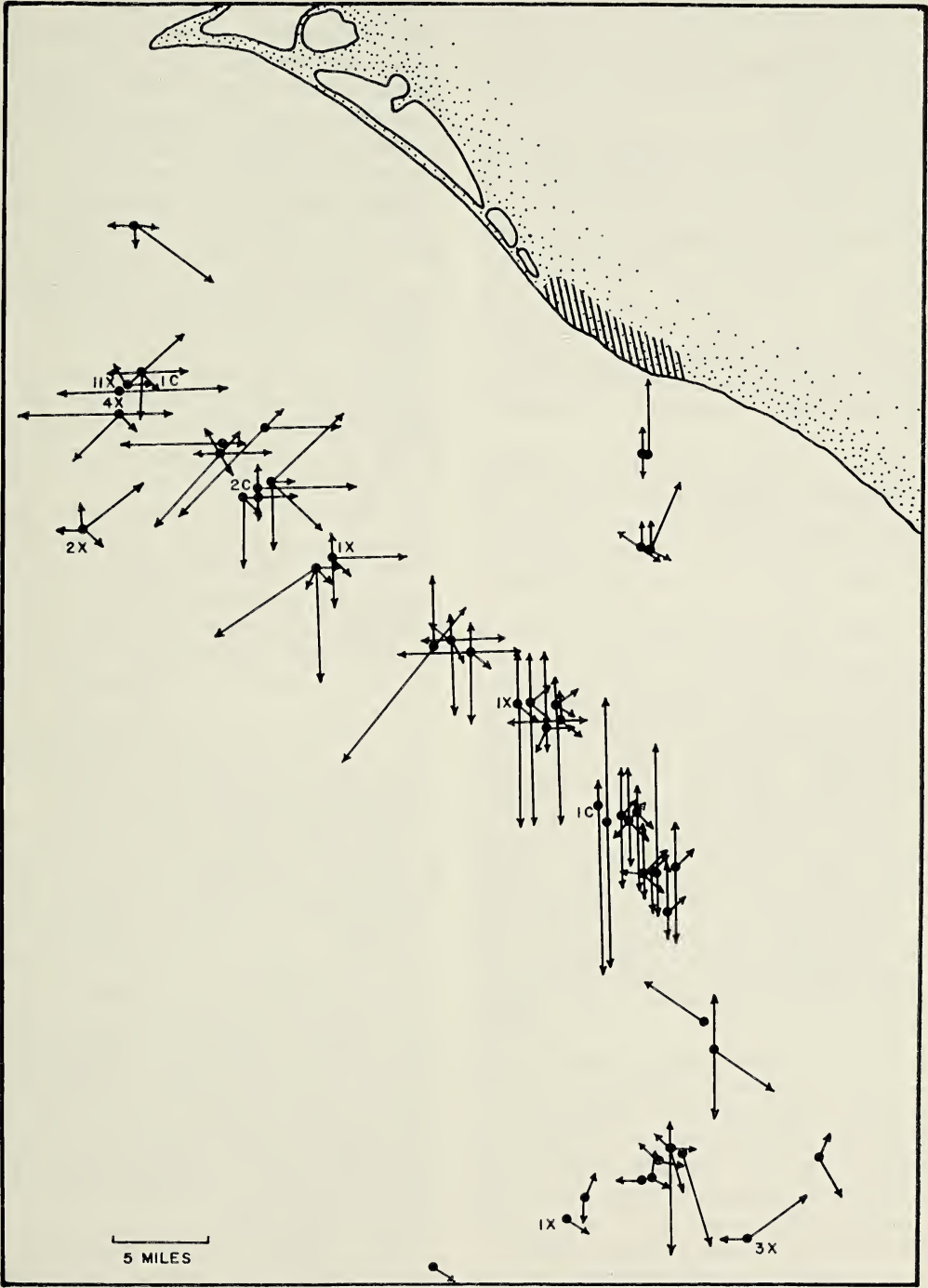
FIG. 18.   Inset from Figure 17. Symbols as in Figure 17. *Cross hatching* indicates the location of the **Cape** Thompson breeding cliffs.

lap of feeding areas may sometimes occur near Point Hope. No particular portion of the ocean off the cliffs seems to be favored for feeding. Comparison of distribution with bottom types (Sparks and Pereyra, 1960:7a) does not reveal clear correlations.

Movements of murres in the open sea within about 40 miles of the nearest colony are strongly oriented by the location of the nesting colony and are little influenced by winds. Regardless of wind direction, murre flight is overwhelmingly oriented either toward or away from nesting areas (Figs. 17 and 18). Beyond the limit of daily feeding flights (about 40 miles), no significant flight trends are evident, in response either to weather or to colony location.

Local or short-term orientations to winds may be striking. Takeoffs from both water and cliffs are made into the wind whenever possible. In the immediate area of the nesting cliffs, flight patterns of murres approaching the cliffs are perceptibly influenced by winds. Several authors whose observations were made mostly from shore have noted flights of murres influenced by wind. Alexander (1935:299) observed feeding flights of Thick-billed Murres near Dungeness Point in England which usually proceeded against the wind. The same author reiterates that movements are related to winds but are more related to tides and currents. Fay and Cade (1959:123) suggest that movements of murres at St. Lawrence Island are correlated with tidal currents. Alexander (1935:299) stated that birds are carried by water currents away from the feeding waters and fly back to regain their initial position. In the Cape Thompson area, however, neither tides nor currents are strong and probably have little influence on murre movements. It is possible in the Cape Thompson area that winds may play the same displacing role that water movements may play elsewhere. Strong winds are common in the area, and Harrison (1955: 110) and several others have noted unusual flights of alcids following strong winds.

At Cape Thompson, flocks of murres coming in often approach the coastline 1 or 2 miles downwind from their nesting location and fly against the wind relatively close to shore. Under foggy conditions, which are especially common when the sea ice is still present, the murres appear to use the shoreline as a guide and fly only a few feet above the beach. While flying against the wind, murres, like many other species fly lower where friction with the substrate slows the air movements. Willoughby at sea and members of the shore party all repeatedly observed this tendency.

Often, birds approaching the cliffs begin to gain altitude when about 5 miles from shore. Birds leaving the cliffs at this distance from shore generally fly lower than those approaching the cliffs, often within a few feet of the water.

Flocks of murres, both approaching and leaving the cliffs, are largest close to the cliffs, although flocking of the departing birds seems to take place farther out to sea than does the breaking up of arriving flocks. Flocks flying away from the cliffs break up as the distance from the colony increases, as though the birds spread out to fill in the areas away from the breeding center. Viewed from the shore, approaching flocks are seen to retain their integrity until single birds or groups of birds break off to occupy their own nesting cliffs. This is most conspicuous at the ends of the colonies, where V-shaped flocks flying along the coastline can be seen to gradually lose their identity while flying along the nesting cliffs.

Four Thick-billed Murres were shot at sea. A male and a female were shot on August 22 at 67°53′N, 166°09′W; both showed evidence of having bred. A male and a female were shot on August 20 at 67°38′N, 165°45′W. The male was molting into the winter plumage but, from the presence of a regressing brood patch and testes still somewhat enlarged, presumably had bred. The female was molting extensively. It possessed no brood patch, and the ovary and follicles were minute; this was probably a nonbreeding bird. Tuck (1961:82–119) presented data which seem to indicate that most murres seen far at sea are young which have not yet reached breeding age.

Both Shuntov (1961:1059–1061) and Jacques (1930:357) observed Thick-billed and Common Murres. Beyond the implication that murres were abundant, only Shuntov (1961: 1059–1061) offered observations of real value in working out the broad outlines of murre

distribution and movement in this area. He stated that both species have similar patterns and that the main wintering waters are located between the edge of the ice and the Alaska Peninsula, primarily in Bristol Bay extending out to Unimak Island, but also extending into the North Pacific. Later (in June), these birds seemed to follow the recession of the ice north toward Bering Strait. He described some of these movements in considerable detail.

Pigeon Guillemot (Cepphus columba)

Two individuals of this species were seen from the "Brown Bear"; one bird just off Cape Lisburne and one at the southern limit of the pack ice, 70°50′N, 165°30′W. An unidentified guillemot was seen near the latter Pigeon Guillemot (Fig. 11). Apparently Shuntov (1961: 1059–1061) did not observe this species. Although Jacques (1930:357) observed it, apparently he saw it only in waters south of the Diomedes. Curiously, Jacques (1930:356–357) observed Black Guillemots (C. grylle) in considerable numbers north of Bering Strait even up to Herald Island, while none were observed on the "Brown Bear" cruise.

Kittlitz's Murrelet
(Brachyramphus brevirostris)

Three sightings of this species, totaling four birds, occurred in the open ocean north of Cape Lisburne. Another bird was seen close to shore in this area at about 69°50′N, 164°33′W (Fig. 11). Neither Shuntov (1961: 1058–1069) nor Jacques (1930:353–366) observed this species.

Parakeet Auklet (Cyclorrhynchus psittacula)

This species is doubtfully recorded from Kotzebue Sound. Several individuals were seen and tentatively identified as Parakeet Auklets (Fig. 11). Both Jacques (1930:356) and Shuntov (1961:1061) cited this species, but it is not clear in either case where the sightings were made. Shuntov (1961:1061) implied that this species, in common with Crested Auklets and Least Auklets, was seen near coastlines but seldom in the open sea.

Crested Auklet (Aethia cristatella)

Two sightings of this species, totaling six individuals, were made about 18 miles west of Cape Thompson, but most observations were made farther south. Hundreds were seen in Bering Strait near their breeding sites on the Diomedes. A single Crested Auklet was seen off Port Clarence (Fig. 11). Many auklets were observed on the voyage which could not be identified positively because of poor visibility. This was particularly true in Bering Strait near the Diomedes. Jacques (1930:356) observed this species near the Diomedes but did not definitely identify it farther north.

Least Auklet (A. pusilla)

Least Auklets were observed on August 26 only in and near Bering Strait, where they occurred in considerable numbers. Visibility was poor at the time, with waves up to 10 ft high and winds gusting up to 40 mph from the northwest, and accurate determination of abundance was not possible (Fig. 11). This is the only area in which Jacques (1930:356) observed them.

Horned Puffin (Fratercula corniculata)

This species was found almost everywhere that murres were found (Fig. 11) but in much smaller numbers. Horned Puffins did outnumber murres in the vicinity of Puffin Island in Kotzebue Sound, where the cliffs apparently support large numbers of puffins but few murres. Data on feeding areas are inconclusive, but it appears likely that puffins resemble murres in this respect. The observations from the "Brown Bear" are at variance with those of Shuntov (1961:1061) and Jacques (1930: 355) in that sightings were common far from shore.

Tufted Puffin (Lunda cirrhata)

This species was rarely seen except near Cape Thompson, Cape Lisburne, and the Bering Strait area (Fig. 11). It is not an abundant breeder at Cape Thompson (Swartz, 1966). It is more numerous at Cape Lisburne and reached its greatest abundance in the vicinity of the Diomedes. Curiously, Shuntov (1961: 1059–1061) seems not to have observed this species. Jacques (1930:355) often did observe it in the Bering Sea and near the Diomedes, but did not list it north of the Diomedes.

Yellow Wagtail (Motacilla flava)

This Old World species has become well established as a breeding species in Alaska (Gabrielson and Lincoln, 1959:692) and migrates back and forth from the Asian mainland. Pelagic observations are to be expected in the migration season, but it is somewhat startling to make three such observations in early August (August 7, 10, and 13) and in such a pattern as to imply that the birds make little or no effort to move along shore to the point closest to Siberia before flying out over the sea (Fig. 10).

To my knowledge, no other authors have reported this species from offshore.

Water Pipit (Anthus spinoletta)

The single doubtful pelagic observation of the Water Pipit is difficult to evaluate (Fig. 10). In view of the doubt which exists as to its identity, it is futile to speculate on the significance of the observation.

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Branchial Muscles in Representatives of Five Eel Families[1,2]

GARETH J. NELSON[3]

DURING THE EVOLUTION of eels the gill arch skeleton of some forms was profoundly modified in gross structure. The modifications are adaptive and are associated with body form and feeding habits of eels (Nelson, 1966). The present paper deals with the musculature attached to the gill arch skeleton of eels representing five families, primarily of the suborder Anguilloidei. Six genera were chosen for study: *Conger* (Congridae), *Anguilla* (Anguillidae), *Moringua* (Moringuidae), *Kaupichthys* (Xenocongridae), *Uropterygius*, and *Gymnothorax* (Muraenidae). The gill arch skeleton of these forms shows a progressive reduction of elements, showing probable stages in the evolutionary development of the specialized "pharyngeal jaws" of the morays—eels of the family Muraenidae.

Gill arch musculature in eels has been studied previously only in *Anguilla* by Dietz (1912) and again by Kesteven (1943). Muscle terminology in the present work follows Vetter (1878) and Edgeworth (1935) as far as possible. Names of gill arch elements are abbreviated as follows: B, basibranchial; H, hypobranchial; C, ceratobranchial; E, epibranchial; I, infrapharyngobranchial; LP, lower pharyngeal tooth plate; UP, upper pharyngeal tooth plate. Gill arches in eels are discussed in detail elsewhere (Nelson, 1966).

MATERIAL AND METHODS

Muscles were dissected in preserved adult specimens and illustrated for *Conger marginatus, Anguilla rostrata, Moringua javanica, Kaupichthys diodontus, Uropterygius knighti,* and *Gymnothorax petelli.* Observations on re-

lated genera (those listed in Nelson, 1966) suggested that the six genera selected for study are representative of the families or subfamilies to which they belong. All material was obtained from the collections of the Department of Zoology, University of Hawaii. With the exception of specimens of *Anguilla,* study material originally was collected by means of shallow water rotenone poisoning around Oahu and Christmas Island.

The illustrations show the muscles in approximately their relative size and positions. Muscles attaching to structures other than gill arches are shown transected. Occasionally other muscles are shown with parts removed to reveal underlying structures. Roots of the branchial arteries are included in the illustrations, for they serve as convenient landmarks, separating adjacent muscles. Bertmar (1962) and Petukat (1965) have dealt with the ontogeny and comparative anatomy of these vessels in some other teleostean fishes.

RESULTS

Conger

Ventral muscles are shown in Figure 1 and listed in Table 1. Obliqui (O1–3) occur on arches 1–3, extending between cerato- and hypobranchials. O3 has its insertion apparently transferred anteriorly to H2. A rectus (R4) is present only between arches 3–4, extending between the proximal ends of C4 and H3. It probably represents part of the oblique of arch 4 with the insertion anteriorly transferred to H3. A rectus communis (RC) extends from the proximal end of C4, with some of its fibers inserting on H3, others on H2 in common with O3. An anterior transversus (AT) extends between the proximal ends of C4 of either side. Extending posteriorly from C5, a single pharyngo-clavicularis (PC) attaches to the cleithrum. A posterior transversus (PT) extends between the distal ends of C5 of either side. An adductor (A5) joins the distal ends

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[2] Contribution No. 261, Hawaii Institute of Marine Biology. Manuscript received May 6, 1966.

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TABLE 1
MUSCLES ATTACHED TO THE VENTRAL PARTS OF THE GILL ARCHES IN SOME EELS*

GENUS	O1	O2	O3	R1	R2	R3	R4	RC	AT	PT	PC	S	VR	A5	SP
Conger	X	X	X	–	–	–	X	X	X	X	X	X	X	X	–
Anguilla	X	X	X	–	X	X	X	X	X	X	X	X	X	X	–
Moringua	X	X	X	–	–	–	X	X	X	X	X	X	X	X	X
Kaupichthys	–	–	–	–	–	–	X	X	X	X	X	X	X	X	X
Uropterygius	–	–	–	–	–	–	–	–	–	X	X	X	X	–	X
Gymnothorax	–	–	–	–	–	–	–	–	X	X	X	X	X	–	X

* A5, Adductor 5; AT, transversus anterior; O1–3, obliqui 1–3; PC, pharyngo-clavicularis; PT, transversus posterior; R1–4, recti 1–4; RC, rectus communis; S, sphincter oesophagi; SP, subpharyngealis; VR, retractor ventralis. X, Muscle present; –, muscle absent.

of C4–5. A sphincter (S) encircles the esophagus and also interconnects C5 of either side. Internal to the sphincter extend longitudinal fibers tending to separate anteriorly, forming a paired muscle, the ventral retractor (VR), attaching to LP and posteriorly extending some distance in the esophageal wall.

Dorsal muscles are shown in Figure 2 and listed in Table 2. External levators (EL1–4) occur on arches 1–4, extending between the cranium and the proximal ends of E1–4. Internal levators (IL1–2) occur on arches 1–2. IL1 extends between the fascia of the trunk and I2. Inferior obliques (IO2–3) interconnect E1–3. A small accessory oblique (AO) extends between E1 and I2. A superior oblique (SO) extends between E3 and I3. An adductor (A4) extends between E4 and C4. A posterior oblique (PO) extends between E4 and C5. The sphincter (S) encircles the esophagus and its anterior portion extends between the arches of either side. Internal to the sphincter occurs a longitudinal layer tending to separate anterior, forming a paired muscle, the dorsal retractor, attaching to UP4 and posteriorly extending some distance in the esophageal wall.

Anguilla

Muscles are shown in Figures 3 and 4 and listed in Tables 1 and 2. They are rather similar to those of *Conger* and have been studied by Dietz (1912) and Kesteven (1943), whose terminologies are compared with that used here in Tables 3 and 4. In the second arch, that portion of the oblique (O2) inserting on H1 corresponds to a rectus (Table 1, R2). A posterior transversus (Table 1, PT) is represented by the anteroventral portion of the sphincter (S).

Moringua

Muscles are shown in Figures 5 and 6 and listed in Tables 1 and 2. A major feature of the musculature is the subpharyngealis (SP), a sheet of longitudinal fibers dorsal to the ventral arch elements. A transverse (Fig. 6, TD) is partly distinct from the anterodorsal part of the sphincter.

Kaupichthys

Muscles are shown in Figures 7 and 8 and listed in Tables 1 and 2. With some minor differences the muscles are most similar to those of *Moringua*.

TABLE 2
MUSCLES ATTACHED TO THE DORSAL PARTS OF THE GILL ARCHES IN SOME EELS*

GENUS	EL1	EL2	EL3	EL4	IO1	IO2	IO3	AO	IL1	IL2	SO	PO	A4	DR	S	MP	LP	PP
Conger	X	X	X	X	–	X	X	X	X	X	X	X	X	X	X	–	–	–
Anguilla	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	–	–	–
Moringua	X	X	–	X	X	X	X	–	X	X	X	X	X	X	X	–	–	–
Kaupichthys	X	X	X	–	X	X	X	–	X	X	X	X	X	X	X	–	–	–
Uropterygius	–	–	–	–	–	X	X	–	X	–	–	–	X	X	X	X	–	X
Gymnothorax	X	X	X	–	X	X	X	–	X	X	–	–	X	X	X	X	X	–

* A4, Adductor 4; AO, obliquus inferior accessorius; DR, retractor dorsalis; EL1–4, levatores externi 1–4; IL1–2, levatores interni 1–2; IO1–3, obliqui inferiores 1–3; LP, protractor lateralis; MP, protractor medialis; PO, obliquus posterior; PP, protractor posterior; S, sphincter oesophagi; SO, obliquus superior. X, Muscle present; –, muscle absent.
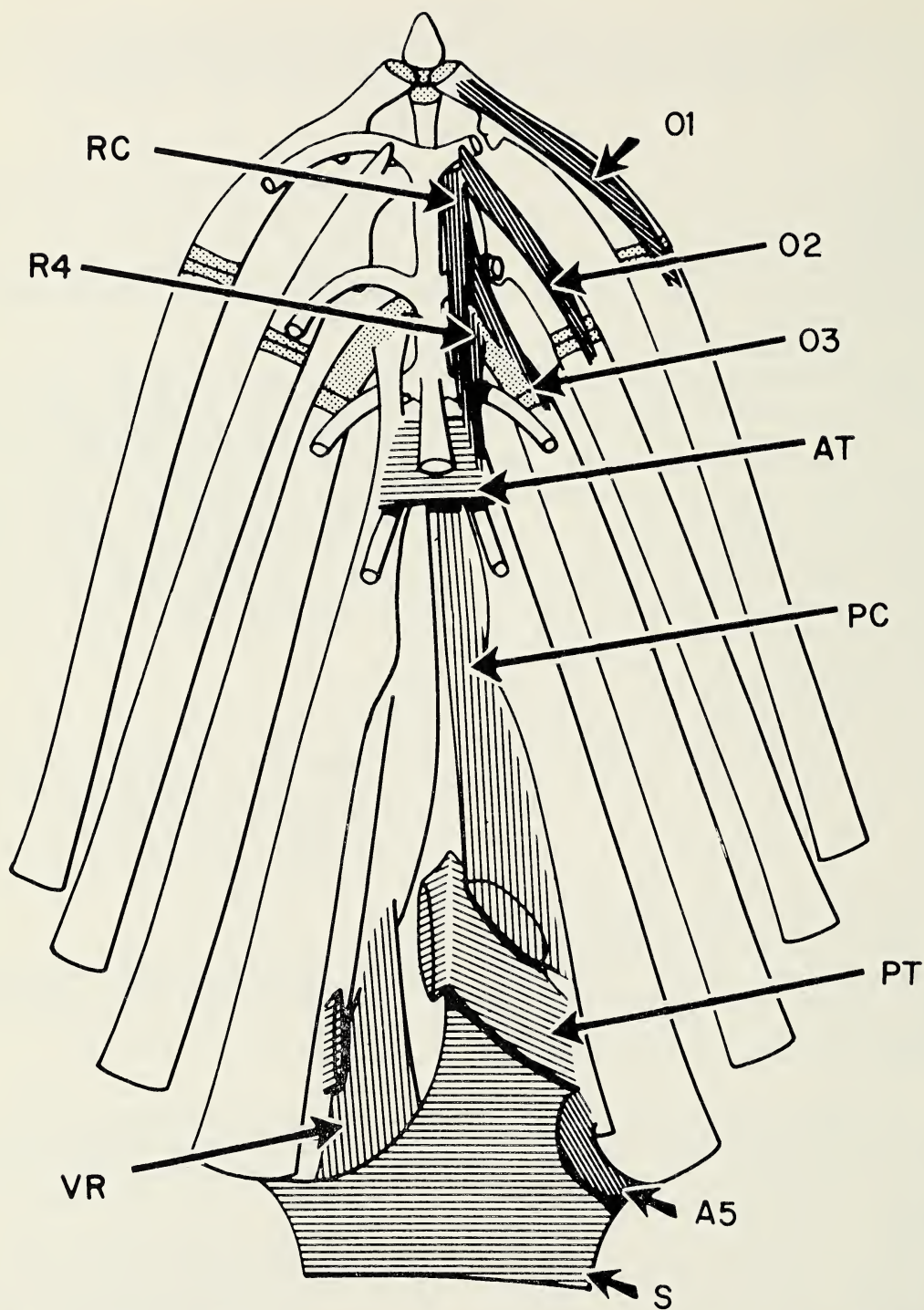
Fig. 1. *Conger marginatus*, ventral gill arch muscles of left side, ventral view, showing roots of afferent branchial arteries. *A5*, Adductor 5; *AT*, transversus anterior; *O1–3*, obliqui 1–3; *PC*, pharyngo-clavicularis; *PT*, transversus posterior; *R4*, rectus 4; *RC*, rectus communis; *S*, sphincter oesophagi; *VR*, retractor ventralis.
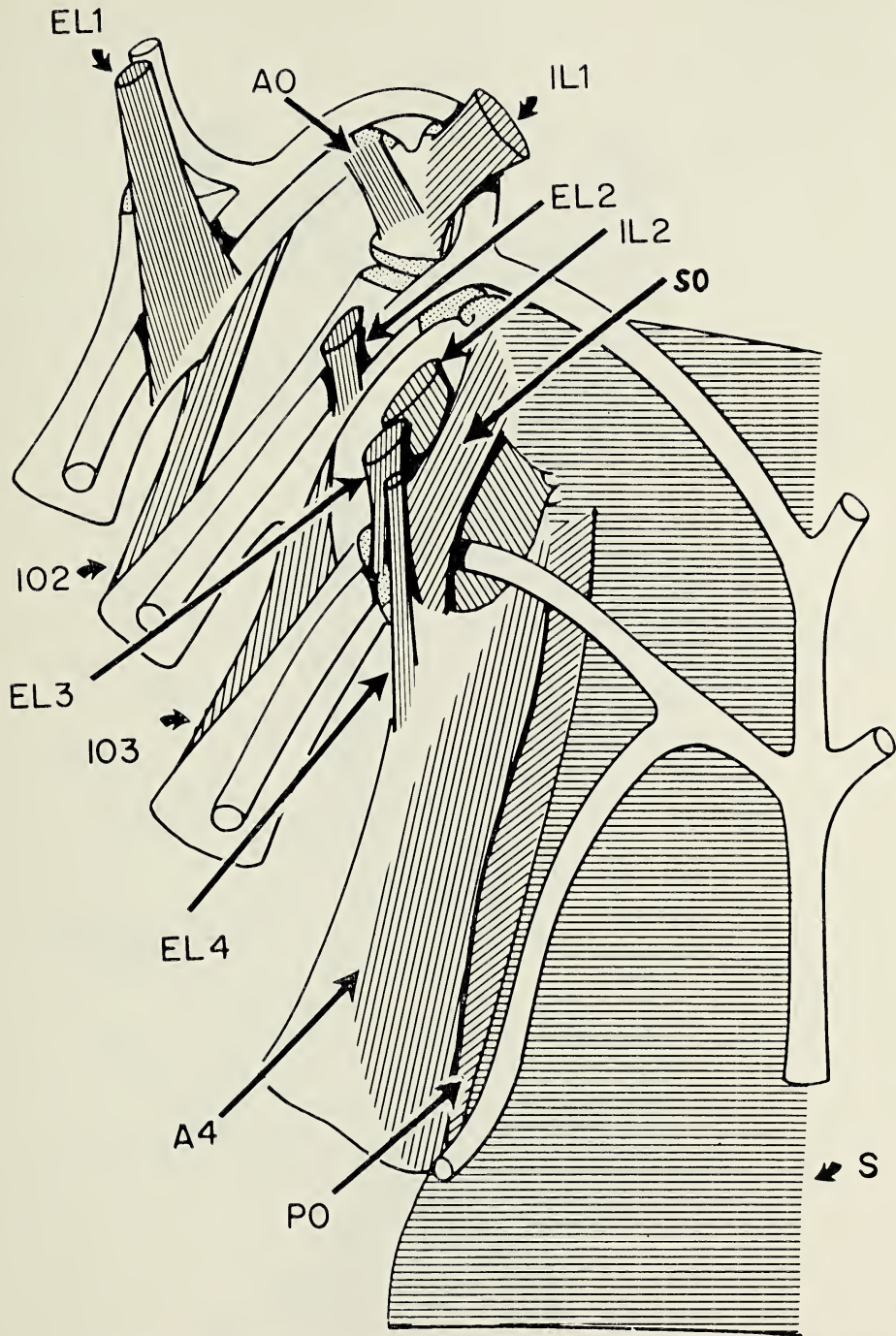
FIG. 2. *Conger marginatus*, dorsal gill arch muscles, dorsal view of left side, showing parts of efferent branchial arteries. *A4*, Adductor 4; *AO*, obliquus inferior accessorius; *EL1–4*, levatores externi 1–4; *IL1–2*, levatores interni 1–2; *IO2–3*, obliqui inferiores 2–3; *PO*, obliquus posterior; *S*, sphincter esophagi; *SO*, obliquus superior.
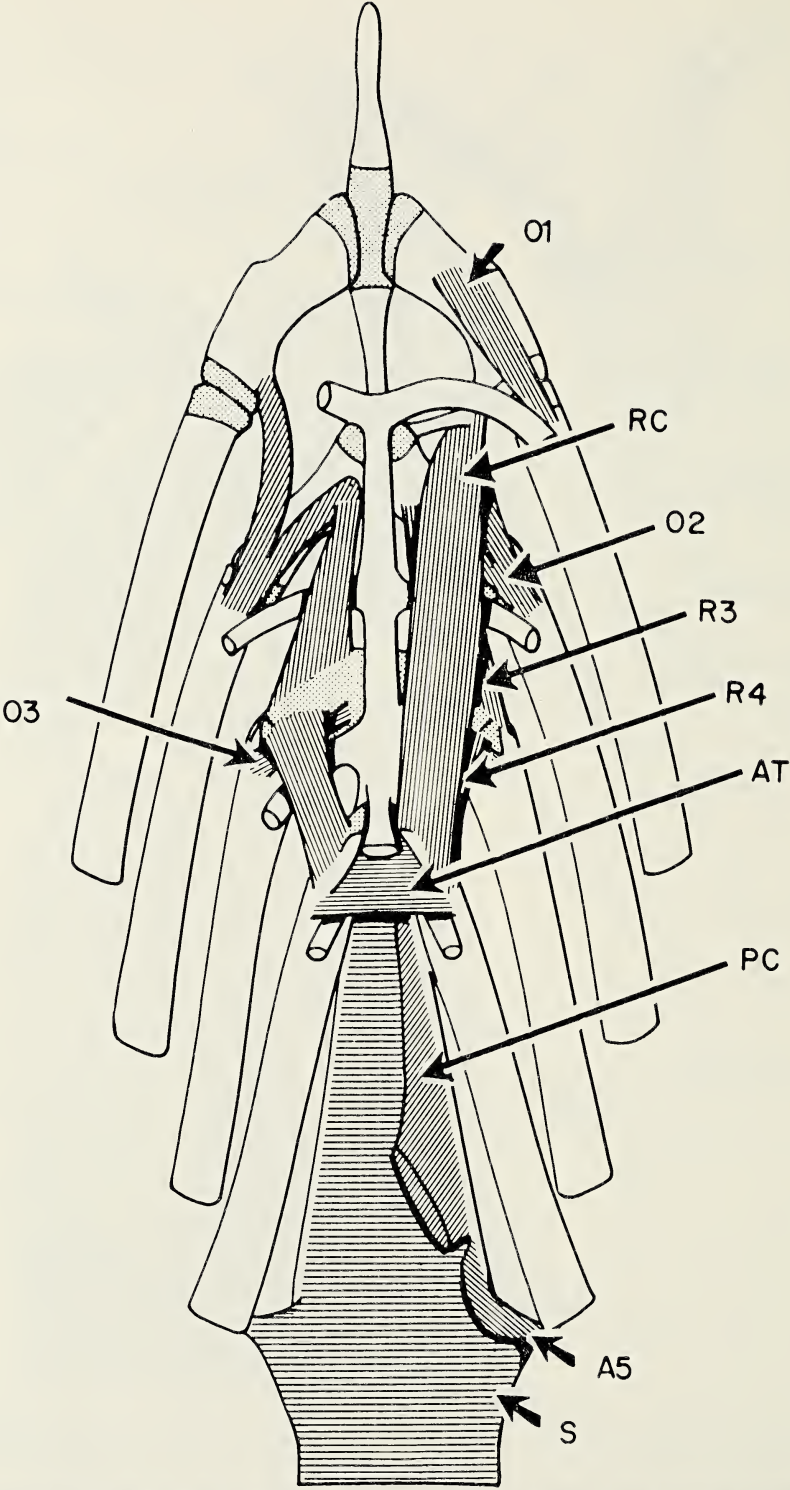
FIG. 3. *Anguilla rostrata,* ventral gill arch muscles, ventral view, with some of those of right side omitted, and showing roots of afferent branchial arteries. Muscles as in Figure 1.
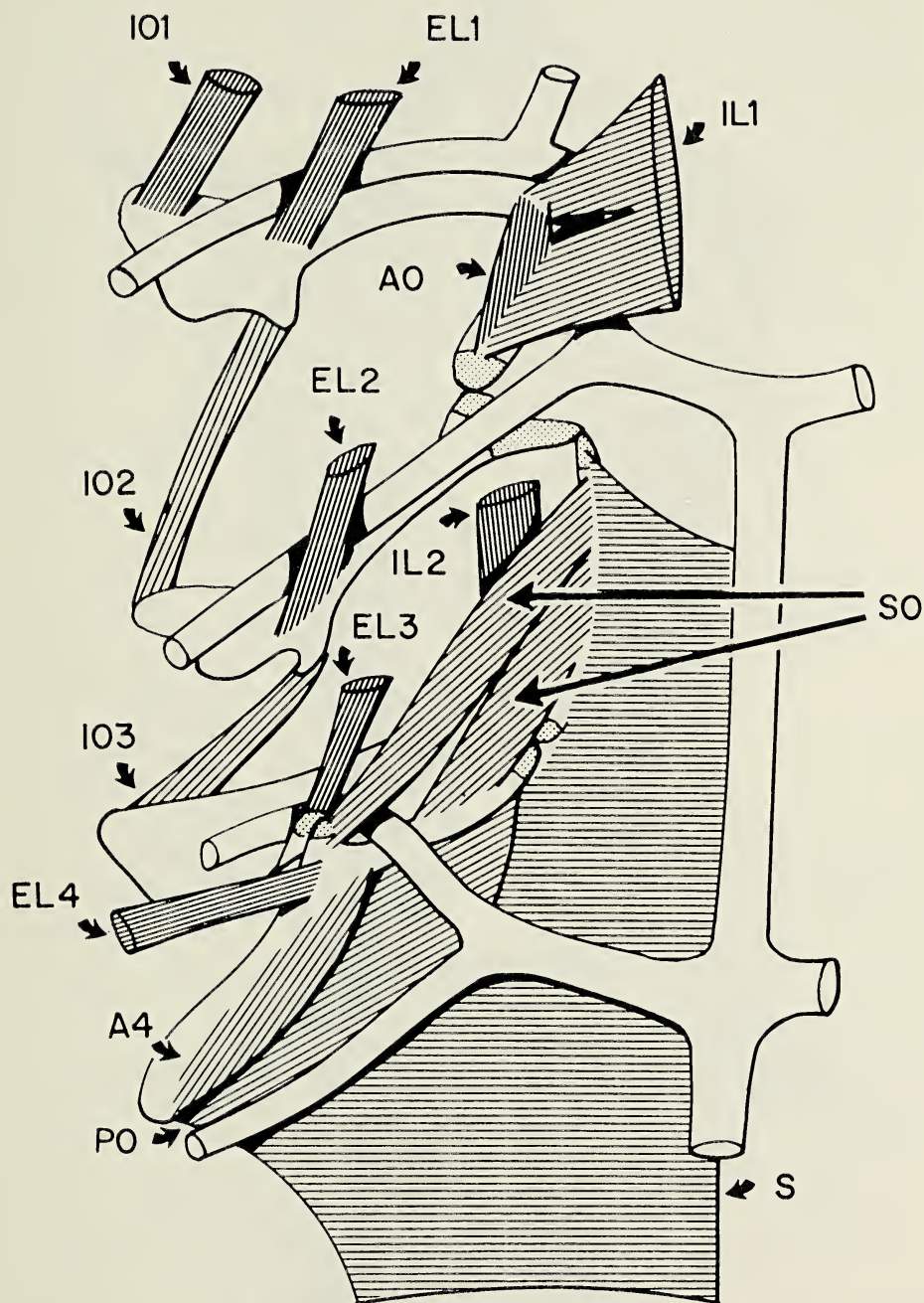
FIG. 4. *Anguilla rostrata,* dorsal gill arch muscles, dorsal view of left side, showing parts of efferent branchial arteries. Muscles as in Figure 2.
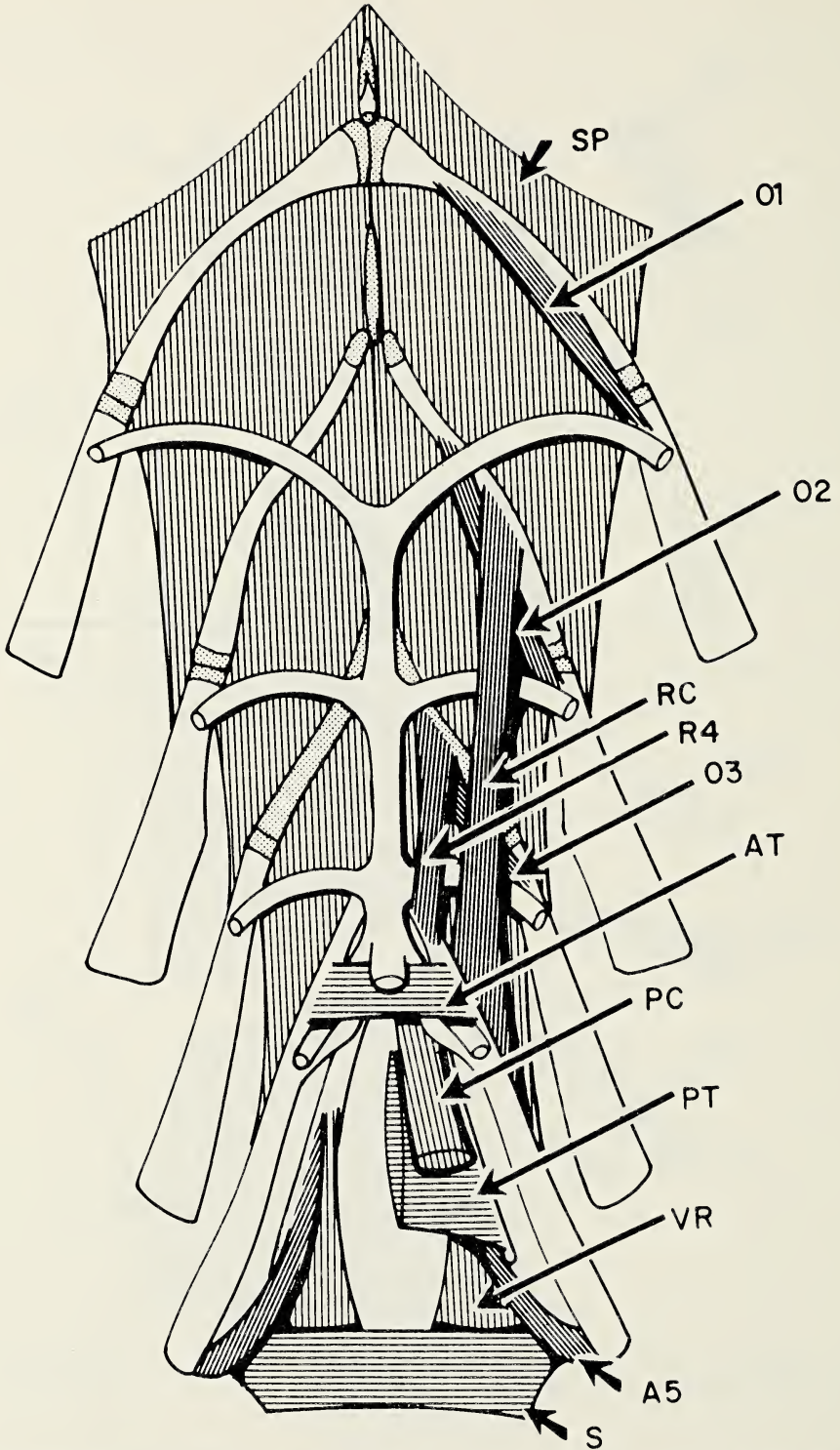
FIG. 5. *Moringua javanica,* ventral gill arch muscles, ventral view, with some of those of right side omitted, showing roots of afferent branchial arteries. *SP,* Subpharyngealis. Other muscles as in Figure 1.
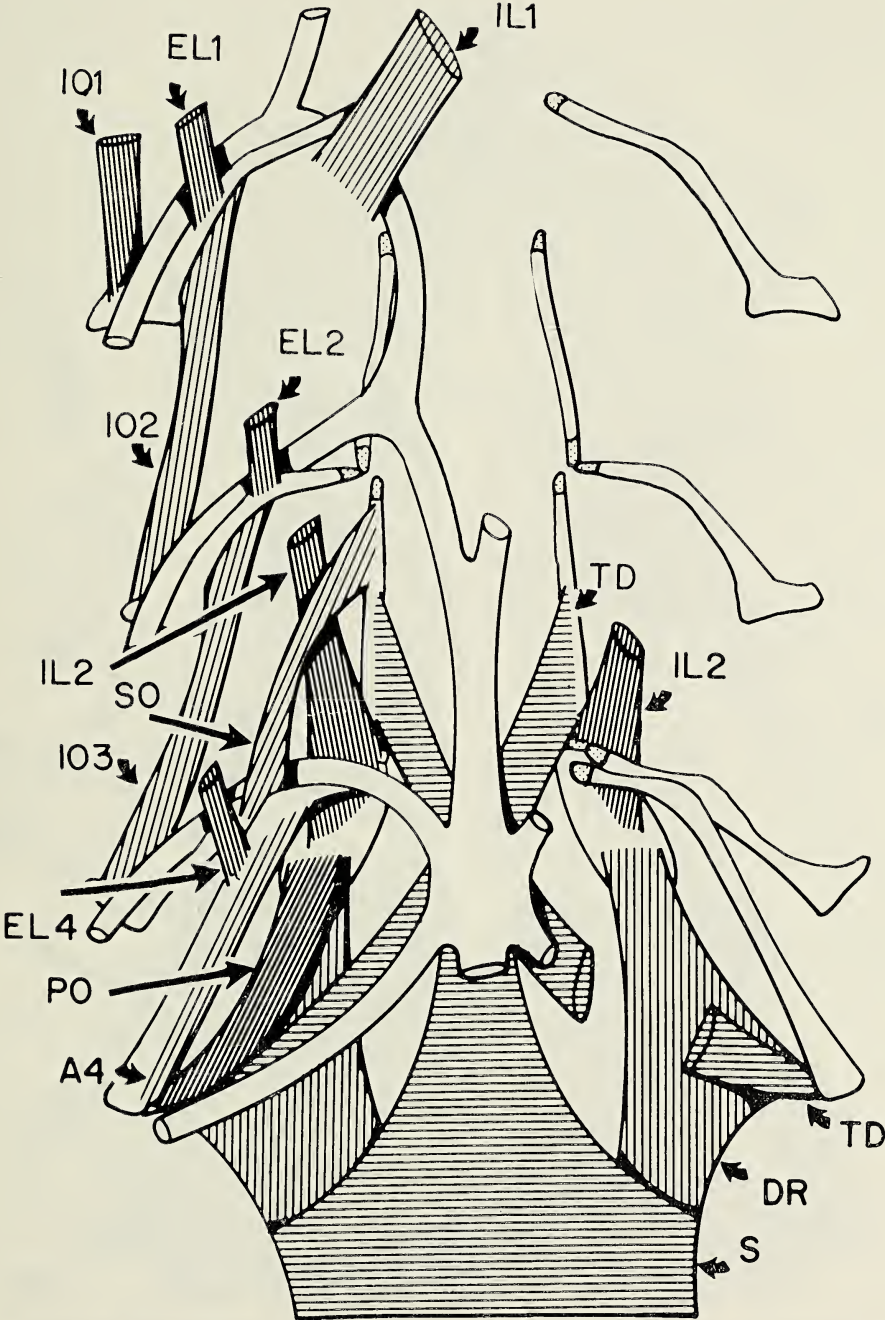
FIG. 6. *Moringua javanica*, dorsal gill arch muscles, dorsal view, with some of those of right side omitted, showing parts of the efferent branchial arteries. *DR*, Retractor dorsalis; *TD*, transversus dorsalis. Other muscles as in Figure 2.
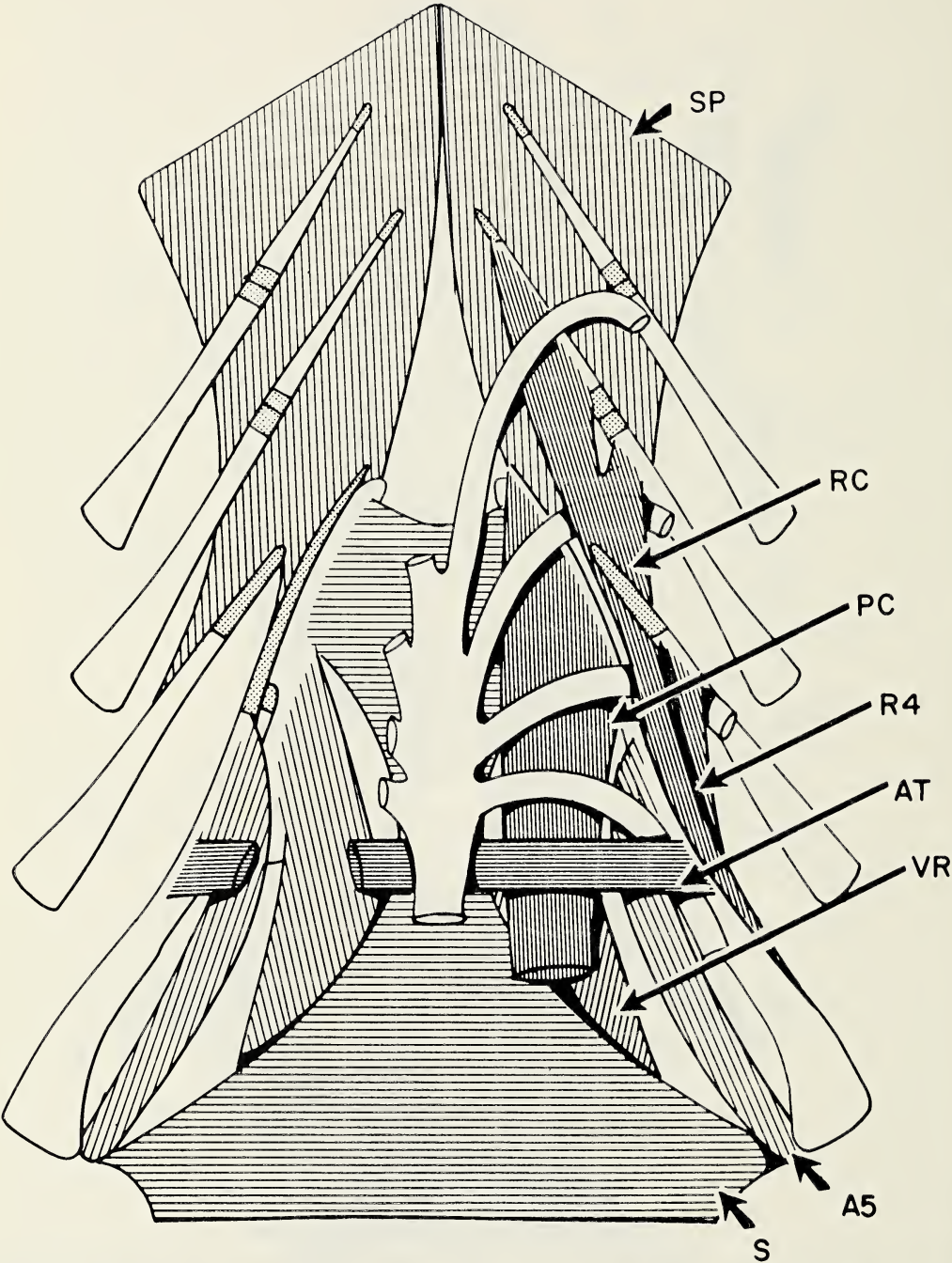
FIG. 7. *Kaupichthys diodontus,* ventral gill arch muscles, ventral view, with some of those of the right side omitted, and showing roots of afferent branchial arteries. Muscles as in Figures 1 and 5.
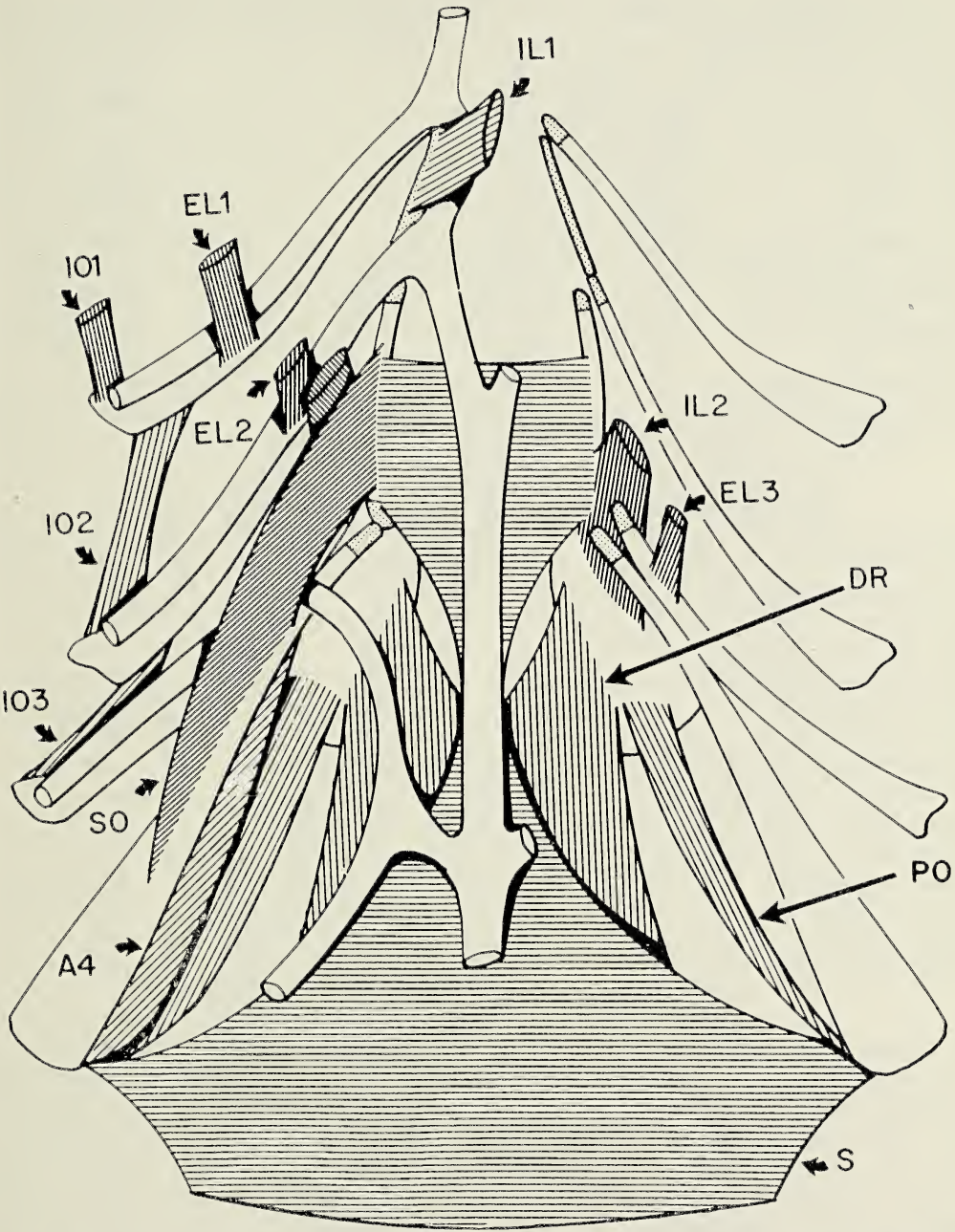
FIG. 8. *Kaupichthys diodontus*, dorsal gill arch muscles, dorsal view, with some of those of right side omitted, and showing parts of efferent branchial arteries. Muscles as in Figure 2.

TABLE 3
MUSCLE TERMINOLOGY FOR VENTRAL GILL ARCH MUSCLES IN *Anguilla*

PRESENT TERMINOLOGY	DIETZ (1912)	KESTEVEN (1943)
Obliquus 1 (O1)	Obl. I	Subarc. obl. 1
Obliquus 2 (O2)	Obl. II	Subarc. obl. 2
Obliquus 3 (O3)	Obl. III	Subarc. obl. 3
Rectus 2 (R2)	Interarc. I/II	none
Rectus 3 (R3)	Interarc. II/III	none
Rectus 4 (R4)	Interarc. III/IV	none
Rectus communis (RC)	Interarc. I/IV	Rectus
Transversus anterior (AT)	Trans. IV	Transversus
Transversus posterior (PT)	Trans. V	Transversus
Pharyngo-clavicularis (PC)	Phar.-clav. ex. + int.	Clav.-pharyng. ext.
Adductor 5 (A5)	none	none
Retractor ventralis (VR)	none	none
Sphincter oesophagi (S)	Pharynxmuskulatur	Sphincter oesophagi

TABLE 4
MUSCLE TERMINOLOGY FOR DORSAL GILL ARCH MUSCLES IN *Anguilla*

PRESENT TERMINOLOGY	DIETZ (1912)	KESTEVEN (1943)
Levator externus 1 (EL1)	Lev. ext. I	none
Levator externus 2 (EL2)	Lev. ext. II	Lev. ext. 2
Levator externus 3 (EL3)	Lev. ext. III	Lev. ext. 3
Levator externus 4 (EL4)	Lev. ext. IV	Lev. ext. 4
Levator internus 1 (IL1)	Lev. int. I?	Retractor dorsalis
Levator internus 2 (IL2)	Lev. ext. IV	Lev. int.
Obliquus inferior 1 (IO1)	Obliq. inf. hy/I	none
Obliquus inferior 2 (IO2)	Obliq. inf. I/II	none
Obliquus inferior 3 (IO3)	Obliq. inf. II/III	none
Obliquus inferior accessorius (AO)	none	none
Obliquus superior (SO)	Obliq. sup. ant.	Epiarc. obl. 1
Obliquus posterior (PO)	Obliq. dors. post.	Epiarc. obl. 2
Adductor 4 (A4)	none	none
Retractor dorsalis (DR)	none	none

Uropterygius

The ventral muscles are similar to those of *Kaupichthys* but are reduced in number (Table 1). The dorsal muscles are shown in Figure 9. Levators are lacking, having been replaced it seems by two new muscles, one extending between the cranium and UP3–4, the medial protractor (MP), the other extending between the cranium and E4, the posterior protractor (PP).

Gymnothorax

The ventral muscles are similar to those of *Uropterygius* with the exception of the sub-

pharyngealis, which appears subdivided into many parts (interbranchial attractors). These are shown in Figure 10. The dorsal muscles (Fig. 11) resemble those of *Kaupichthys* more than those of *Uropterygius*. However, they do include a medial protractor. They include in addition a lateral protractor extending between UP3–4 and the ventral part of the hyoid arch, attaching there in common with the ventral muscles LA1, OA1–2. The dorsal retractors attach in common with the ventral retractors to the ventral surfaces of the 13th–15th vertebrae.
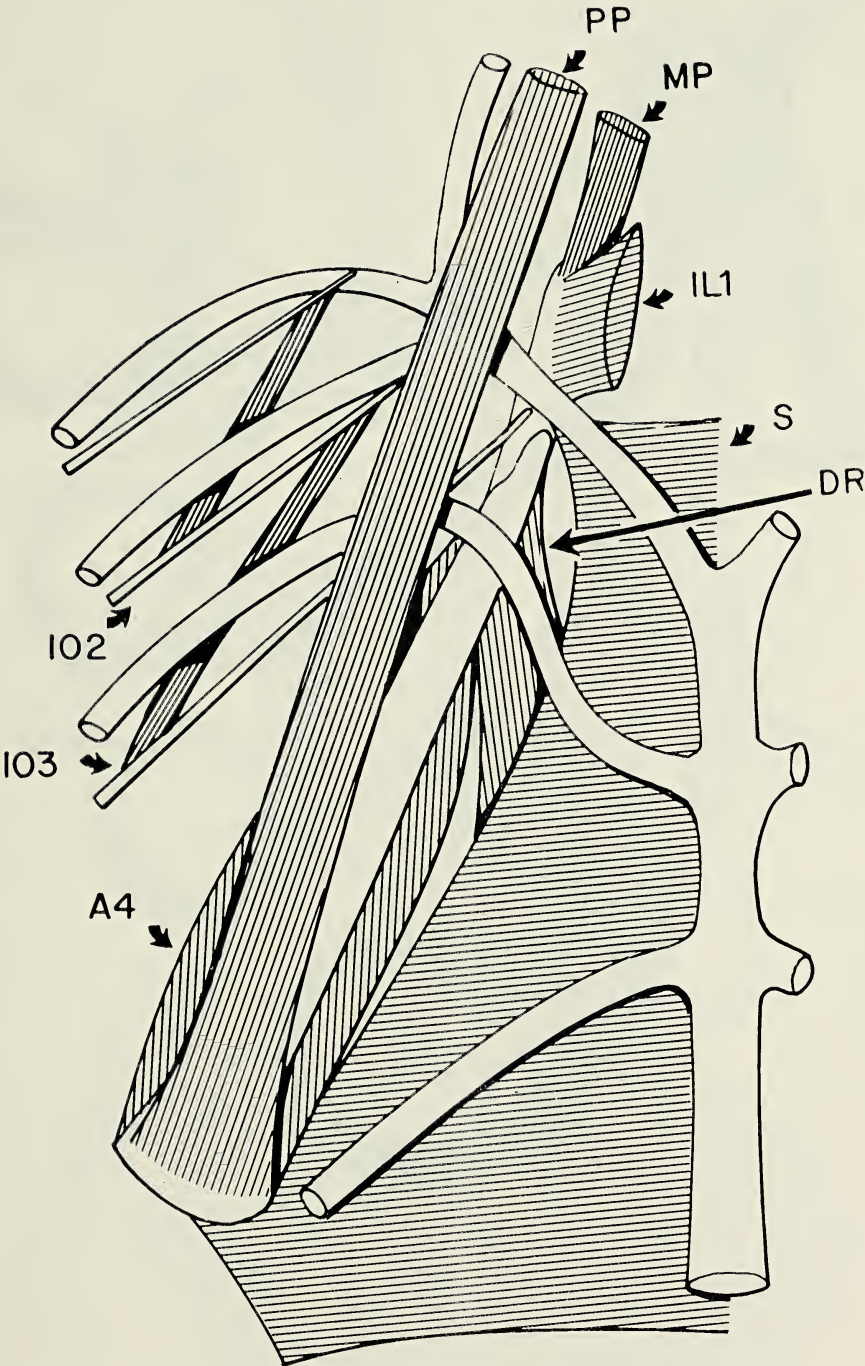
FIG. 9. *Uropterygius knighti*, dorsal gill arch muscles, dorsal view of left side, showing parts of efferent branchial arteries. *MP*, Protractor medialis; *PP*, protractor posterior. Other muscles as in Figure 2.
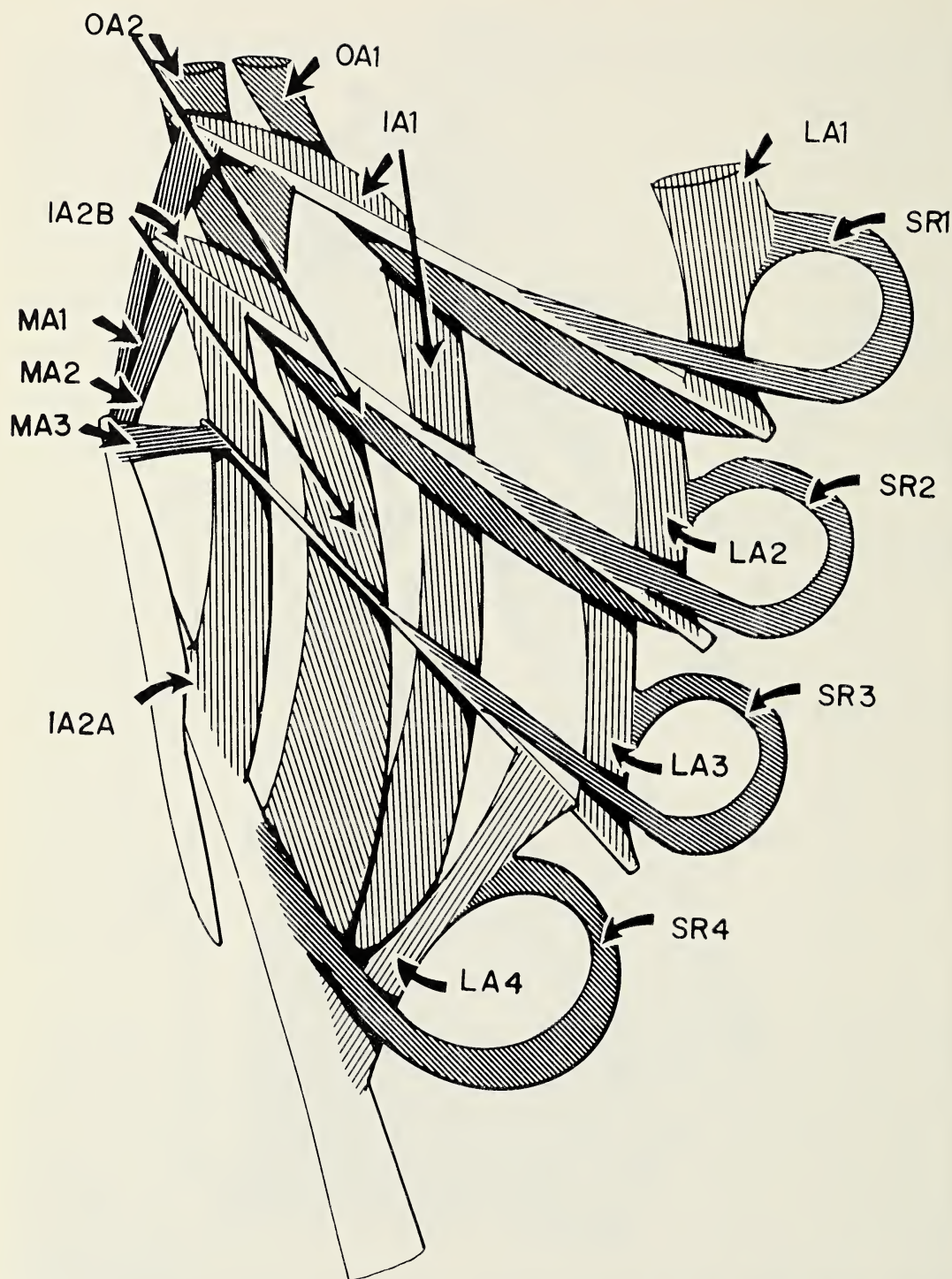
Fig. 10. *Gymnothorax petelli*, some of the gill arch muscles of the left side, ventral view, showing subdivisions (attractores interbranchiales and sphincteres branchiales) of the subpharyngealis. *IA1–2*, Attractores intermediales 1–3; *LA1–4*, attractores laterales 1–4; *MA1–3*, attractores mediales 1–3; *OA1–2*, attractores obliqui 1–2; *SR1–4*, sphincteres branchiales 1–4.
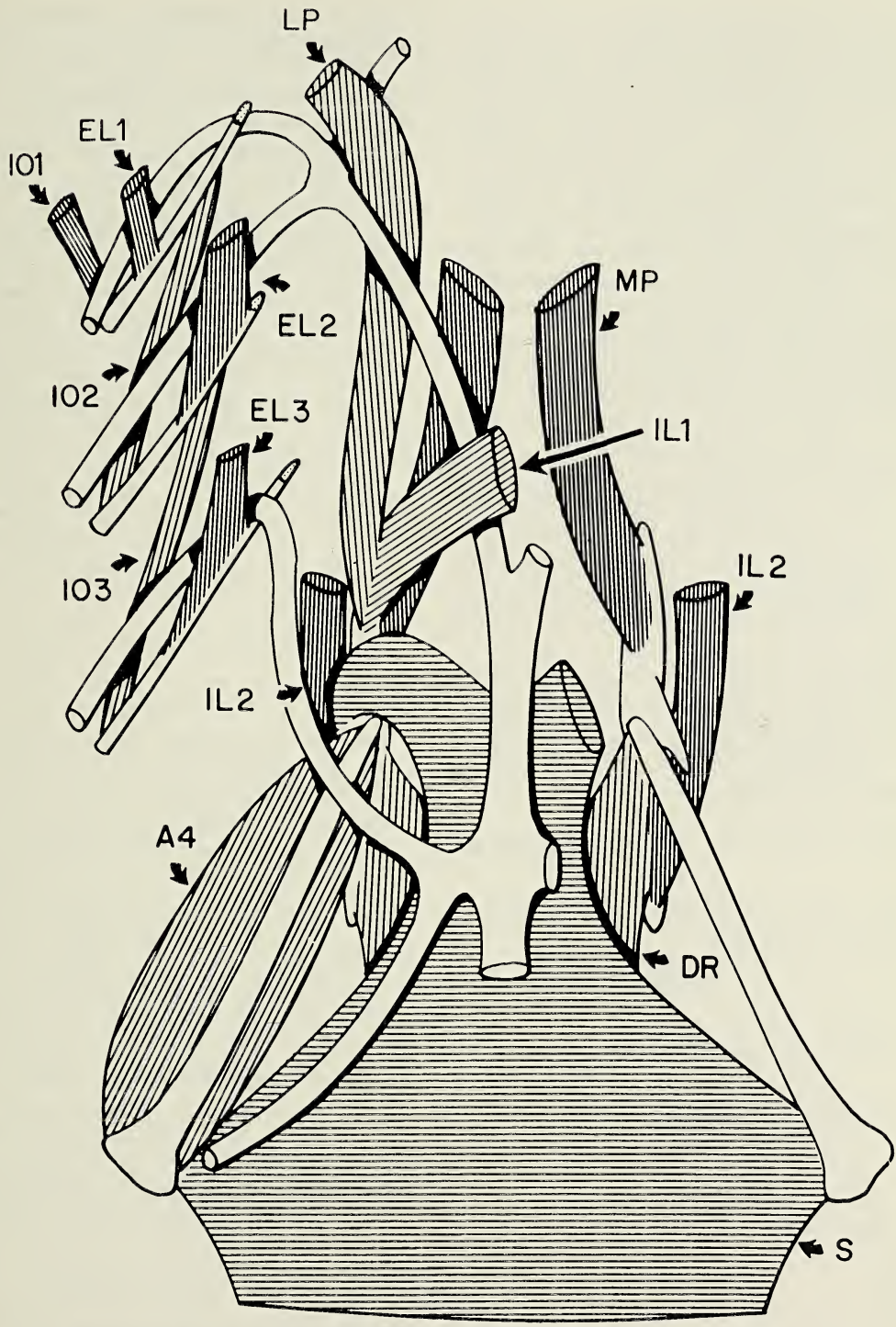
FIG. 11. *Gymnothorax petelli,* dorsal gill arch muscles, with some of those of the right side omitted, and showing parts of efferent branchial arteries. *LP,* Protractor lateralis; *MP,* protractor medialis. Other muscles as in Figure 2.

DISCUSSION

If they are represented by the rather linear reduction in gill arch elements, relationships among the examined genera may be as diagrammed in Figure 12. Thus, *Conger* would be the most primitive and *Gymnothorax* the most advanced. Gill arch muscles of *Conger* are not structurally far removed from those of *Elops* (Nelson, 1967) or those of other generalized lower teleostean fishes (Vetter, 1878; Dietz, 1912, 1914, 1921; Greene and Greene, 1913). On the other hand, the muscles of *Uropterygius* or *Gymnothorax* are far removed structurally from those of *Conger* and consequently appear to be advanced rather than primitive. The series of studied forms ranging from *Conger* to *Gymnothorax* shows a progressive series of muscle modifications, involving the loss of some muscles and the appearance of others (Tables 1 and 2). The series of muscle modifications in a general way parallels the linear reduction in gill arch elements of these forms.

Particular modifications of gill arch muscles in eels seem correlated with particular modifications of the gill arches themselves. Reduction of ventral musculature (obliqui and recti) parallels reduction in ventral arch elements

FIG. 12.   Diagram of possible relationships among some eels.

(basi- and hypobranchials). Appearance of protractors and enlargement of the retractors and their attachment to the vertebral column in muraenines parallel the enlargement of the fourth arch and the tooth plates it supports.

The appearance of the subpharyngealis is not so easily correlated with any particular modification of the gill arch skeleton. It appears, seemingly, in place of the obliqui and recti. However, nothing is known of its embryonic development and it may or may not represent modified obliqui or recti. Its position is distinctive, being internal to the skeletal elements rather than external as are the obliqui and recti. Probably the ventral musculature shifted from a relatively external to a relatively internal position with the reduction and loss of basibranchials. In any event, it assumed a sheetlike form, gradually encroaching upon the gill slits, which in the more advanced eels (e.g., the muraenids) are reduced to small round openings.

Dorsal and ventral paired retractor muscles are present in all of the eels examined. In most forms they are only partly distinct subdivisions of the inner longitudinal muscle layer of the anterior esophagus. In eels of the subfamily Muraeninae, they acquire an attachment to the vertebral column.

The taxonomic significance of retractors in other groups of bony fishes has been dealt with by Dietz (1912, 1914, 1921) and Holstvoogd (1960, 1965). According to Nelson (1967), retractors probably have developed an attachment to the vertebral column independently in many evolutionary lineages of bony fishes. Probably in each lineage they are associated with and constitute part of an improvement or specialization in the feeding mechanism.

It is hardly to be doubted that the attachment to the vertebral column has been acquired independently among the eels. No other group having retractor muscles has both dorsal and ventral retractors attaching in common to the vertebral column. Indeed, except among eels, ventral retractors seem to be lacking. Thus, the attachment to the vertebral column of muraenines no doubt is another example of independent development. In this case they attach to the tooth plates of the pharyngeal
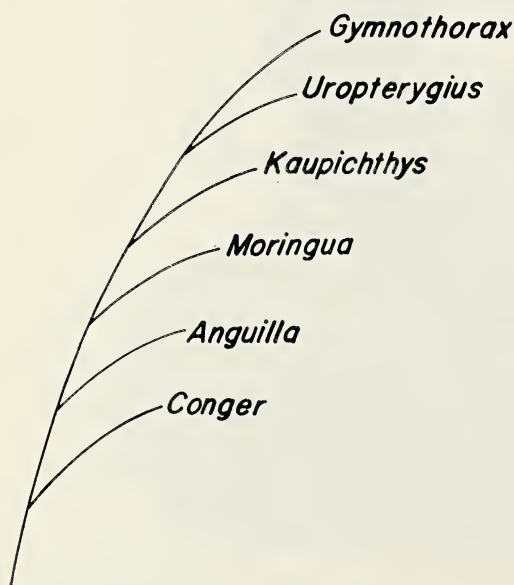
jaws and apparently constitute, with the pharyngeal jaws, an advancement or specialization in the feeding mechanism.

The common course and attachment of the retractors, both ventral and dorsal, to the vertebral column in morays are evidence that the muscles act together, simultaneously retracting both upper and lower tooth plates. Indeed, the construction of the plates and their supporting bones prohibits independent movement of the ventral and dorsal plates. Protraction probably occurs through the contraction of the subpharyngealis and the dorsal muscles joining the cranium and gill arches. Protraction and retraction probably succeed one another during the swallowing of prey. It is likely that, in the morays, the pharyngeal jaws and the muscles attached to them enable these forms to transport relatively large prey from the jaws into the esophagus, a distance which in eels is secondarily lengthened (Nelson, 1966). Thus, these structures appear to be adapted to the known predatory habits of the morays.

SUMMARY

1. Branchial muscles are described for six genera representing five eel families: *Conger* (Congridae), *Anguilla* (Anguillidae), *Moringua* (Moringuidae), *Kaupichthys* (Xenocongridae), *Uropterygius* and *Gymnothorax* (Muraenidae).

2. In the examined forms, muscles as well as gill arches suggest stages in an evolutionary sequence, with the Congridae being the most primitive and the Muraenidae being the most advanced.

3. Dorsal and ventral retractor muscles occur in all species examined. In eels of the subfamily Muraeninae they acquire secondarily an attachment to the vertebral column.

4. Gill arch muscles and pharyngeal jaws of muraenids are adaptations probably enabling these fishes to swallow large prey.

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Acoustical Behavior of the Menpachi, *Myripristis berndti*, in Hawaii[1]

MICHAEL SALMON[2]

ABSTRACT: The menpachi (*Myripristis berndti*) is found in aggregations inside caves and under ledges during the day in water more than 3 m deep. Diel tape recordings in these areas showed that the fish produced four types of sounds (knocks, growls, grunts, and staccatos), with no crepuscular peaks, from dawn to dusk. At night, when the fish scattered to feed, few sounds were detected.

A fifth sound was produced when fish were hand-held. The sound-producing mechanism was determined by a series of ablation experiments on hand-held fish. It consisted of a pair of bilateral muscles attached to the skull anteriorly and the air bladder, the first two dorsal ribs, and the cleithrum bone posteriorly.

Populations of 6–7 fish were maintained in the laboratory in large tanks with an artificial cave. They remained inside the cave during the day but swam actively throughout the tank at night. Brief chasing of a small fish by a larger, accompanied by knocking sounds, was frequently observed. Growl sounds were produced during more intense aggressive interactions between two fish of about the same size. There was no evidence of territoriality by members of any population.

Few grunt or staccato sounds were produced when various species of nonpredatory fish were introduced among laboratory populations. Many of these sounds were elicited when moray eels were introduced.

Sound playbacks to four populations from one of two speakers on either side of the cave elicited different responses depending on the sound tested. All fish immediately turned to and moved toward the experimental speaker when grunt or staccato sounds were played. Some fish briefly turned to the experimental speaker when knocks were emitted but none moved to the source. There was no detectable change in behavior when background noise was played back.

Three fish tested in an aktograph showed increases in locomotory activity at night which corresponded with periods of nocturnal scattering and feeding in field populations.

The acoustical system of the menpachi is compared with that of the longspine squirrelfish, *Holocentrus rufus*, an Atlantic species.

THE "MENPACHI" consist of four species of economically important fishes in the Hawaiian area. Although their habits are well known to trap- and spearfishermen, there have been few published studies on their ecology and none on their acoustical behavior. In this report the behavior correlated with or stimuli eliciting four types of sounds (grunts, staccato, knocks, and growls) produced by *Myripristis berndti* (Jordan and Evermann) are described. A fifth sound, produced when fish were hand-held, was physically analyzed in conjunction with experiments to determine the sound-producing mechanism. Diel patterns of locomotory and feeding activity in nonreproductive groups of *M. berndti*, and their relationship to sound production were determined by field and laboratory observations. Experiments were carried out to determine the response of laboratory populations to playbacks of their own sounds and to other fish species commonly associated with them in their coral reef community.

It has been known for many years that several species of squirrelfishes (family Holo-

centridae) produce sounds. Studies to date have been made on two species in the genus *Holocentrus*. Fish (1948) first reported sound production in the group. Moulton (1958) studied *H. ascensionis* in Bimini and described two types of sounds produced in the field, a single sound (the grunt) and one composed of several thumplike sounds produced in a series (the staccato). Winn, Marshall, and Hazlett (1964) were the first to study the significance of these sounds experimentally. They found that the nonreproductive social organization of *H. rufus,* which produced the same types of sounds as *H. ascensionis,* was territorial. When a conspecific individual entered the territory of another squirrelfish, the resident produced many grunt sounds and rarely staccatos, sometimes acompanied by fin erection, nipping, and lateral displays in which the two fish moved parallel to each other. Intruders of other species elicited both staccatos and grunts, but more staccatos were produced toward larger fish or a potential predator, such as a moray eel. Laboratory populations were maintained in large tanks and each fish defended a territory consisting of the inside of a large can, open at one end, and the area immediately before the opening. When staccato sounds were played back to these populations from one of two speakers on each side of the tank, the fish at first retreated into their cans. Some then swam to the sound source, while others turned their heads toward the speaker from just outside the can, indicating that the fish were probably able to localize the source of sound. Diel recording showed that more sounds were produced during the day than at night, when the fish were active and feeding. Peaks in sound production occurred at dawn and dusk. It was hypothesized that the peaks were caused by movements of nocturnal and diurnal species into and out of the reef and through the territories of squirrelfishes under conditions of reduced light intensity.

Moulton (1958) stated that contractions of the body wall musculature associated with the first three ribs and the air bladder were responsible for sound production in *H. ascensionis.* In a series of ablation experiments, Winn and Marshall (1963) showed that the muscles involved in sound production were bilateral and attached to the posterior part of the skull, the air bladder, and the first two dorsal ribs in *H. rufus.* Removal of one muscle reduced the intensity of sounds produced by hand-held specimens, but did not significantly change sound duration or number of pulses per sound, indicating that the two muscles contracted simultaneously to produce each sound. Gainer, Kusano, and Mathewson (1965) studied the electrophysiological and mechanical properties of the sound-producing muscle in the same species. The muscle was capable of contracting at a frequency of 100/second with no mechanical summation, while fast white muscle from the same fish showed considerable summation at 50/second.

Myripristis is the second largest genus in the family. These fish live in schools and move over the reef more than do members of the genus *Holocentrus* (Herald, 1961), which are solitary-territorial. Other reports indicate that the schools remain in caves or under ledges during the day and scatter to feed at night (Hobson, 1965). The presence of sand-dwelling annelids in the stomachs of *M. berndti* from the Marshall Islands indicated that the fish move to open areas, away from the reef during nocturnal feeding (Hiatt and Strasburg, 1960).

There have been no published studies on the acoustical behavior of any species in this genus. Nelson (1955) described the antero-bilateral projections of the air bladder which, in *M. argyromus,* completely covered the auditory bullae and were thus more extensively modified, presumably for an auditory function, than in *H. ascensionis* and *H. rufus.*

MATERIALS AND METHODS

All observations and experiments were carried out at Oahu, Hawaii, from February to July 1965. Most of the field observations were made in Pokai Bay, Waianae, in water 3–9 m deep. The study area spanned a 1-km distance along the coast. Several other schools were observed in similar habitats offshore at Black Point and Ilikai Harbor. The topographic features of the habitats and estimates of school size in number of fish were recorded with the aid of an underwater flashlight and drawing pad or were photographed directly with a Nikonos underwater camera.

All tape recordings were made with an Uher 4000-S Report recorder and an Atlantic Research Corp. hydrophone (Model LC-57). Field recordings were carried out by securing a boat with three anchors over the reef area containing a school of fish. The hydrophone was placed inside a cave or under a ledge within 1 m of the fish and was secured with a weight. A small air-filled bottle was attached to the hydrophone cable about 1 m from the water surface to keep the cable taut and prevent entanglement in the reef. Field recordings were made at tape speeds of 2.3 cm/sec ($\frac{15}{16}$ i.p.s.); laboratory recordings were made at 9.5 cm/sec ($3\frac{3}{4}$ i.p.s.).

Specimens 12–20 cm in total length were caught by hook and line or in traps and brought into the laboratory for study under more controlled conditions. They were established in groups of 6–7 fish in 756-liter fiberglass tanks with a plexiglas front, in which a "cave" was constructed with two building blocks covered with a piece of masonite (Fig. 1). Holes in the blocks allowed the fish to enter and leave through the side as well as through the front of the cave. A continuous flow of fresh sea

water circulated through the tank at temperatures between 21° and 23° C. The hydrophone was suspended in front of the cave to record sounds. Behavior correlated with sound production was described immediately after recording the sounds.

Sound playbacks were carried out. One underwater speaker (University MM-2L) was placed on each side of the cave. The sounds used for playbacks were all recorded from previous populations of *M. berndti*. They were played through one of the speakers from a continuous loop of tape on a Crown tape recorder (Model CR-25) which repeated the entire playback every 11 seconds. The response of four populations to grunt, staccato, and knock sounds was determined. Each type of sound was played back once in a random order to each group of fish and at levels comparable to those emitted by the fish. The number of fish on the left or right side of the tank was determined every 15 seconds of a 5-minute period with sounds played back during minutes 2 and 4 from one speaker, selected randomly. Recordings were made during the entire 5-minute period to monitor playbacks and record any sounds produced by the fish. One observer (the recorder) noted the position of the fish in the tank. Another, shielded from both the fish and the recorder, turned the sound on and off through one of the two speakers. The recorder had no prior knowledge of which speaker was being used during the test although the response of fish to certain sounds enabled him to determine the experimental speaker with 100% accuracy.

Various species of fish commonly associated with *M. berndti* in the field were introduced in a random order to seven individual populations. These were: *Myripristis berndti*, *M. argyromus*, *Holocentrus xantherythrus*, *Priacanthus meeki*, *Parupeneus porphyreus*, and *Gymnothorax undulatus*. The type and number of sounds produced by the populations were recorded for a 1-minute period before and during the introduction.

Patterns of locomotory activity were determined for three fish, one for 24, one for 56, and one for 72 hours. The fish were placed singly in a large doughnut-shaped chamber 7.6 cm wide, 9.5 cm deep, and with a mean swimming circumference of 87.6 cm. Fresh aerated
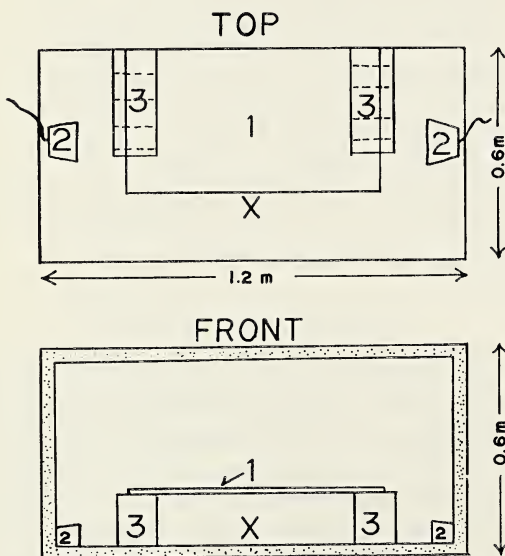
FIG. 1. Top and front views of tank in which laboratory populations were maintained, showing outside dimensions. *1*, Roof of cave; *2*, underwater speakers used in sound playbacks; *3*, building blocks with two holes through which fish could enter and leave the cave through the side as well as by the front opening; *X*, position of hydrophone.

sea water circulated through the chamber at all times. Two Pflueger Fish Finders (Enterprise Manufacturing Co.), placed 180° apart and positioned to face toward the center of the chamber, were used to detect the movement of the fish. The fish finder emits an 800-kc signal as a narrow beam across the chamber. The reflected signal is identical to the emitted one when no moving object is present and, when the signals are compared (heterodyned) in the receiver, they cancel out. Movement of a fish past the fish finder shifted the frequency of the reflected signal and caused a deflection on the chart of a Rustrak event recorder (Model 92). The chamber was placed in a small room within 1 m of a large window, so that the fish was exposed to normal changes in the daily light cycle. For further details concerning the apparatus, see Muir et al. (1965).

A series of ablation experiments was carried out to determine the sound-producing mechanism. All fish produced grunts when hand-held by the caudal peduncle. Sounds of normal hand-held fish were recorded, followed by recordings of the same fish (record level on tape recorder left constant) after removal of the following: one or both sound-producing muscles; other associated muscles and bones; the gas from the swim bladder. All fish were held about 7.5 cm from the hydrophone. Operated fish were anesthetized with MS-222. A few muscle potentials were recorded from the sound producing muscle of two fish with a Tektronix Low Level Amplifier (Type RM-122) and oscilloscope (RM-504) and were photographed with a Grass camera (Model C-4). The sound duration, number of pulses, and interpulse intervals were measured by photographing the recorded sounds from a Fairchild oscilloscope (Model 701) with the Grass camera, at film speeds of 100–500 mm/sec.

The effect of operations on the intensity of sounds was determined. A General Radio Co. Impact-Noise Analyzer (Type 1556-B) was connected to the output of the tape recorder and a peak sound pressure value was determined for a normal fish. The peak sound pressure of the same fish after the operation was also obtained. The peak value for the normal sound was considered as 0 decibel, while the value for the operated fish was considered as positive db (if the value exceeded that of the normal fish) or negative db (if the value was less). Relative sound pressures at various octave band frequences were also measured. The output of a General Radio Co. Octave Band Noise Analyzer (Type 1558-A) was connected to the imput of the impact analyzer. A sine wave of 400 cps was applied to the imput of the octave band analyzer when set in the "all pass" position, and with the preamplifier in the 20 Kcs weighting (essentially flat response from 20 cps to 40 Kcs). The impact analyzer was then calibrated to give a peak value 3 db higher than the root mean square value shown by the octave band analyzer for the sine wave. After calibration, the fish sounds from the tape recorder were applied to the imput of the octave band analyzer and readings were determined from the impact analyzer. The loudest of the first five sounds produced by a normal fish was measured and considered as 0 db. All sound pressures in various octave band frequencies of the first five sounds produced before and after operations on this fish were compared with the 0 db value. The sound pressures of all filtered signals were always less than the 0 db value. The reduction was measured and expressed in decibels. All sound pressures obtained from the impact analyzer were relative to 0.0002 microbar.

The Sound-Producing Mechanism

Sounds produced by hand-held specimens were accompanied by vibrations which could be felt along an area extending from the dorsolateral region of the skull to the side of the body just lateral to the air bladder. The most intense contractions were in the dorsal region behind the eye. Removal of some of the superficial muscles, opercula, and part of the suprascapular bone revealed a band of muscle slightly yellow in appearance, which could be observed to contract synchronously with the production of sound. The muscle was attached to the posterior part of the skull, just above the eye, and passed over the anterior lobes of the air bladder to its insertion point above the area where the main body of the air bladder gives rise to the lobes (Fig. 2). At its insertion, the muscle was attached medially to the first two dorsal ribs and
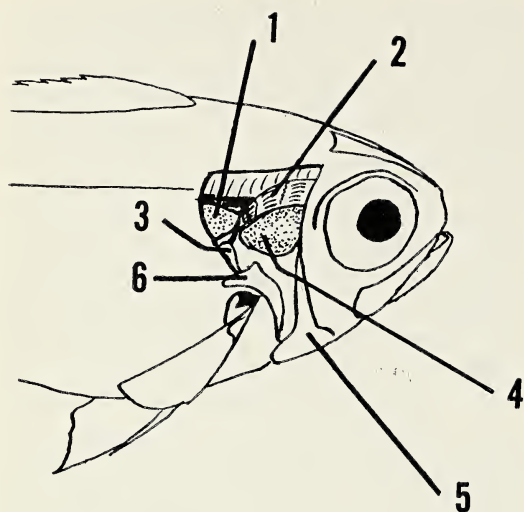
FIG. 2. Anatomy of the sound-producing mechanism and surrounding bones in *Myripristis berndti*. *1*, Main body of swim bladder; *2*, sound-producing muscle; *3*, dorsal portion of cleithrum bone with tendon attached to sound-producing muscle; *4*, anterior lobe of swim bladder; *5*, preoperculum; *6*, scapula.

the air bladder. A small tendon connected the muscle to the cleithrum bone laterally. Another small, flat muscle (not shown in the figure) attached to the skull and ran between the sound-producing muscle and the anterior lobe of the air bladder, to the operculum. This muscle was routinely cut during ablation experiments, with no apparent effect on sound production. The sound-producing muscle was highly vascularized and appeared to be composed of three distinct myomeres.

Removal of one sound-producing muscle resulted in a relative decrease of 2–7 db in operated fish, when compared with their own normal sounds (Table 1). Sound pressures were reduced in all octave bands but were greatest in the 75–150 cps band. Normal sounds contained frequences below 75 cps to under 4,800 cps, with most energy between 300–600 cps. Oscillographs of these sounds are shown in Figure 3.

The temporal patterns of the pulses within these sounds are shown in Table 2. Normal fish produced sounds composed of 7–10 pulses (mean, 8.2). Operated fish showed more variability in pulse range (6–11), and a mean

value of 9.04 pulses per sound. Increases in number of pulses were correlated with increases in sound duration. Interpulse intervals were variable, but in most sounds the intervals between the penultimate and the last pulse were greater than between other pulses. A few muscle potentials recorded from two fish were composed of 6–8 spikes (Fig. 3). The interspike intervals and total duration for a series of spikes were comparable to values for interpulse and total-duration measurements of sounds with the same number of pulses.

The effect of removing the superficial muscles and bones near the sound-producing muscle is shown in Table 3 and Figure 3. The peak pressure of sounds produced by operated fish, when compared with pressures of their own sounds before the operation, increased in one fish, decreased in two, and remained the same in two fish.

Five fish in which both sound-producing muscles were removed produced no audible sounds.

The role of the air bladder in sound production was determined by replacing the gas in the bladder with sea water. Five fish, in which a small hole had been punctured in the lobe of the air bladder with a syringe, continued to produce sounds at intensities comparable to their own normal sounds (mean peak sound pressure = 1.1 db above normal fish). Only a few bubbles of gas escaped through the puncture. When the puncture was held open the intensity of the sounds decreased as gas escaped until finally, when the air bladder was completely filled with water, no audible sounds were produced although the muscles could still be felt to contract. The presence of only a small bubble of gas in the bladder resulted in production of sounds of very low intensity.

Field Observations and Diel Recordings

At least 20 different schools of menpachi were found in the Pokai Bay area. In all cases, these were mixed assemblages of *M. berndti* and *M. argyromus*, from 13 to 23 cm in total length. In shallower waters, *M. argyromus* predominated. Both species were found to produce the same types of sounds and to have similar nocturnal-diurnal activity patterns in

TABLE 1

PEAK PRESSURE CHANGE AND RANGE OF PRESSURES IN OCTAVE BANDS OF FISH SOUNDS BEFORE (NORMAL) AND AFTER (OPERATED) REMOVAL OF ONE SOUND-PRODUCING MUSCLE[1]

CONDITION	PEAK PRESSURE CHANGE IN OPERATED FISH	RANGE OF OCTAVE BAND SOUND PRESSURES IN DB					
		75-150	150-300	300-600	600-1200	1200-2400	2400-4800
Normal	−7 db	19-25	14	4-6	11-12	29-32	39
Operated		36-38	22-24	11-13	14-16	31-33	—*
Normal	−4 db	29-30	13-14	3-5	9-11	24-28	—
Operated		31	17-19	9-11	10-12	27-30	—
Normal	−4 db	26-29	14-17	3-6	9-12	25-29	—
Operated		32-34	17-20	7-9	11-14	22-23	—
Normal	−5 db	28-30	15-17	4-6	9-10	20-22	—
Operated		35	20-22	9-10	13-14	22-23	—
Normal	−2 db	28-30	14-15	4-5	7-9	22-23	—
Operated		31-34	17-19	7-9	7-8	24-26	—

[1] Values represent db *below* total sound energy, so that the smallest reductions represent the octave bands of greatest amplitude.
* Sound pressures below ambient level.

TABLE 2

Total Duration, Number of Pulses, and Interpulse Intervals of Hand-Held Sounds Produced by Five Fish Before (Normal) and After (Operated) Removal of One Sound-Producing Muscle

NO. OF SOUNDS	NO. OF PULSES	AVG AND RANGE OF SOUND DURATION (MSEC)	AVERAGE AND RANGE OF TIME (MSEC) BETWEEN PULSES										
			1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–11	11–12
Normal Fish														
6	7	88.5 80–92	8.7 8–10	14.8 10–22	10.7 8–14	11.0 8–14	11.8 8–13	13.0 9–19					
11	8	94.4 89–104	9.4 8–11	9.7 8–12	11.0 9–13	10.0 8–12	11.2 10–12	11.3 10–13	14.6 11–19				
6	9	103.0 100–106	9.2 8–10	9.7 8–11	10.5 10–12	10.2 10–11	10.2 9–11	10.7 10–12	11.0 10–12	14.7 12–18			
2	10	116.0 114–118	10.0 10	9.0 8–10	11.0 10–12	10.0 10	10.0 10	10.5 10–11	10.5 10–11	11.0 10–12	14.0 13–15		
Operated Fish														
1	6	78.0	10.0	11.0	12.0	12.0	22.0						
2	7	93.0 76–110	9.5 9–10	13.0 10–16	9.5 9–10	14.0 10–18	10.0 10	17.5 13–22					
7	8	104.0 90–160	10.4 9–12	15.0 10–27	10.0 9–11	13.6 10–27	10.3 9–12	15.6 10–42	11.9 10–13				
6	9	101.5 94–101	10.2 8–12	10.3 9–12	10.2 10–11	10.0 9–11	10.7 9–15	10.3 10–12	10.8 10–13	13.2 10–17			
4	10	113.3 108–128	10.8 10–13	10.3 9–11	10.0 9–11	10.0 10	10.0 10	10.0 10	10.0 9–11	11.0 10–12	14.3 12–20		
4	11	114.0 106–124	9.5 8–10	9.5 8–10	9.3 8–10	9.3 8–10	9.5 8–10	9.8 9–10	10.0 9–11	10.3 9–12	11.0 10–12	12.8 11–14	
1	12	125.0	10.0	10.0	10.0	10.0	12.0	10.0	10.0	11.0	10.0	12.0	14.0
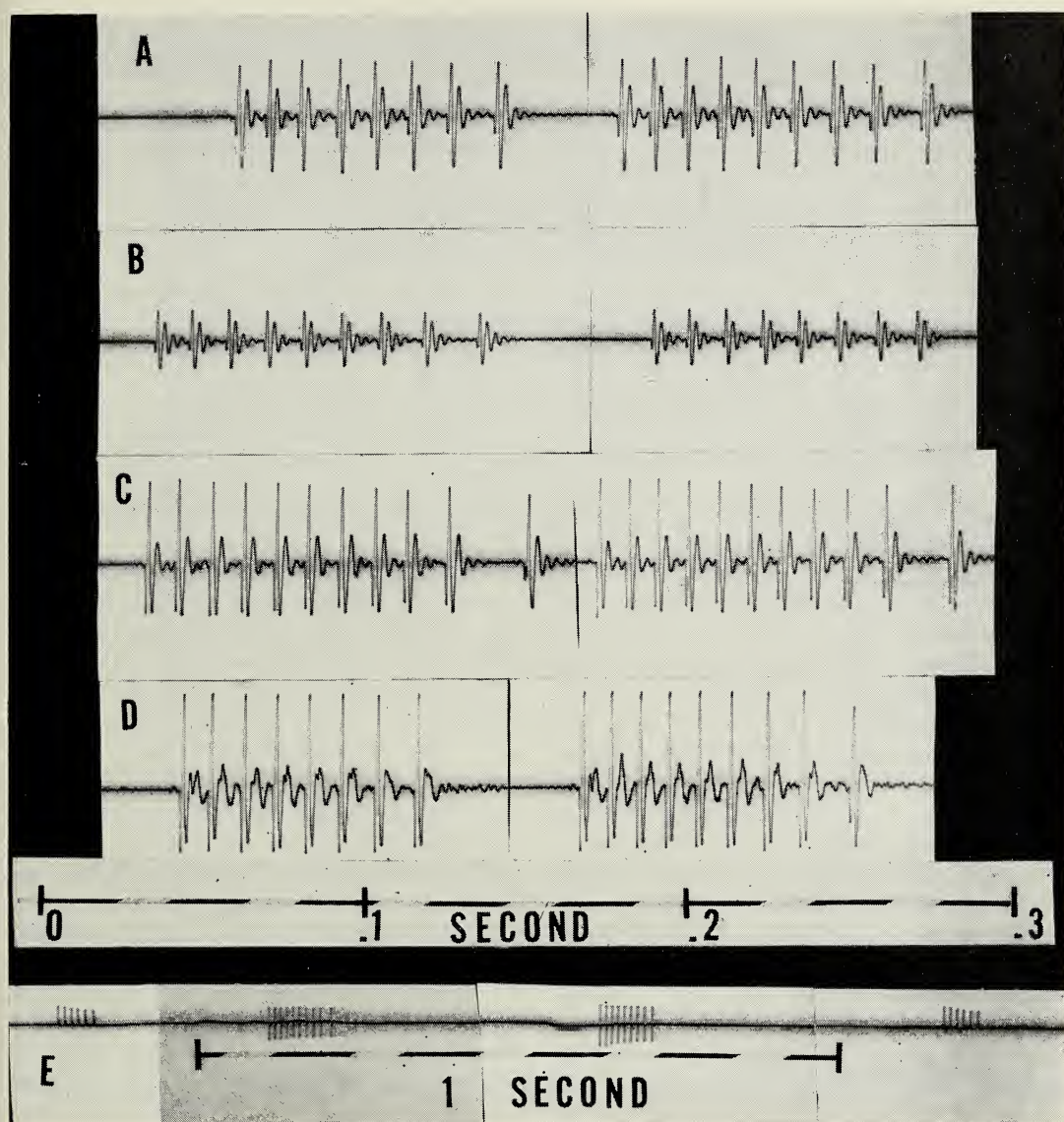
FIG. 3. Oscillographs of grunt sounds and muscle potentials from hand-held *Myripristis berndti*. *A*, Two sounds from a normal fish; *B*, two sounds from the same fish after one sound-producing muscle has been removed. Note decrease in intensity. *C*, Two sounds from another normal fish; *D*, two sounds from the same fish after superficial muscles and bones over one sound-producing muscle have been removed; *E*, muscle potentials corresponding to four hand-held sounds recorded from two other fish.

the field. The schools varied in size from 8 to more than 100 fish, depending upon the space in the area in which they were located. Fish were found in one of three different habitats at depths to 9 m: under ledges which extended 1–6 m deep and 3–20 m long, raised 0.2–1.5 m off the bottom; in caves with openings 1–3 m in diameter and variable inside dimensions; and in recesses within mounds of glomerate coral located within 1–3 m from the bottom. The same types of habitats were occupied by several populations found offshore at Black Point and the Ilikai Harbor.

During 26 days of daytime field observations (between 0800 and 1730 hours) scattered over a 3-month period the presence of schools in

TABLE 3

PEAK PRESSURE CHANGE AND RANGE OF PRESSURES IN OCTAVE BANDS OF FISH SOUNDS BEFORE (NORMAL)
AND AFTER (OPERATED) REMOVAL OF THE MUSCLES AND BONES OVER THE SOUND-PRODUCING MUSCLE

CONDITION	PEAK PRESSURE CHANGE IN OPERATED FISH	RANGE OF OCTAVE BAND SOUND PRESSURES IN DB					
		75–150	150–300	300–600	600–1200	1200–2400	2400–4800
Normal	+2 db	16–18	3–7	5–6	1–4	16–19	31–34
Operated		21–24	8–9	4–6	6	19–20	33–36
Normal	−1 db	23–26	11	4–5	6–7	19	32–33
Operated		29–30	14–15	6–7	10	21–22	36–41
Normal	0 db	23–36	8–12	5–8	5–8	17–20	33–35
Operated		25–27	11–12	6–7	5–6	17–19	30–34
Normal	−1 db	25–27	13–14	7–8	5	19	21–22
Operated		27–28	15–16	8–11	6–7	15–17	32–33
Normal	0 db	29–31	14	6–7	5	16	31–32
Operated		28–30	14	7–9	4–8	16–19	30–32

these habitats was always observed. None of
the fish were ever seen swimming in open
water during the day. Associated with the
schools of menpachi were groups of other
squirrelfish (*H. ensifer, H. xantherythrus,* and
H. spinifer—usually a single specimen),
aweoweo (*Priacanthus cruentatus* and *P.
meeki*), moray eels (*Gymnothorax* sp.), car-
dinal fish (*Apogon* sp.) and pipefish (*Syngna-
thus* sp.). Various other diurnal species of reef
fishes were observed to enter and leave caves
and ledges. The frequent visits of large schools
of goatfish (*Parupeneus* sp.) did not result in
production of staccato and grunt sounds when
the entrances coincided with diel recordings.

It was not possible to carry out detailed ob-
servations on the behavior of menpachi in these
areas, even with SCUBA gear. A diver's pres-
ence resulted in retreat by the fish into darker
and less accessible areas, accompanied by the
production of many staccato and grunt sounds.
Only a few fish briefly investigated the diver
within the first minute or two after he ap-
peared. When the caves or ledges were too
shallow for backward retreat, the school scat-
tered to either side or rushed quickly back and
forth within the confines of the area.

Many menpachi (both *M. berndti* and *M.
argyromus*) were caught with hook and line.
The bait was kept off the bottom, just outside
the ledge or cave opening. No fish were ever
caught or took bait during the day. All 57 fish
caught by fishing during the study period were
captured between 1930 and 2030 hours, al-

though on some nights fishing continued until
midnight.

Tape recordings in the field were carried
out in four different areas of Pokai Bay, three
for a 24-hour and one for a 9-hour period.
The results are shown in Table 4. Four types
of sounds were recorded: (1) staccatos, (2)
grunts, (3) a series of knocking sounds vari-
able both in intervals between consecutive
knocks and in number of knocks in a series,
and (4) growls, consisting of a rapid series of
sounds lasting from 1 to 4 seconds. Oscillo-
graphs of these types of sounds recorded from
laboratory populations are shown in Figure 4.
Only a few of these kinds of sounds were pro-
duced after sunset and before sunrise. Knocks
were the most frequently recorded of all sounds,
with no obvious peaks in rate of production
after an initial increase following dawn. In
one 24-hour recording (April 28–29), there
was a peak in staccato and grunt sounds at dusk.

General Behavior of Laboratory Populations

Laboratory populations confined their day-
time movements to slow swimming inside the
cave, with occasional chasing of one fish by
another. Individual fish occasionally swam out-
side of the cave for a few seconds. When
lights were turned off at night, the movements
of fish could still be detected in the available
ambient light. Within 5 minutes, the fish were
swimming rapidly around the tank above the
cave. Several populations all produced sounds
in the laboratory at night when recordings were

TABLE 4

DIEL PATTERNS OF SOUND PRODUCTION (FIELD) AND LOCOMOTORY ACTIVITY (LABORATORY) IN *Myripristis berndti*

ACTIVITY RECORDED	DATE		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Sound production (four schools)	4/28	Stac.	0	0	0	0	0	0	1	0	0	0	0	18	13	4	6	1	0	2	28	1	0	0	0	0
		Grnt.	0	0	0	0	0	1	0	0	0	0	1	8	11	9	16	14	1	5	20	1	0	0	0	0
		Knck.	0	0	0	0	6	19	12	12	14	21	16	30	37	35	36	16	21	25	39	0	2	0	1	0
		Grwl.	0	0	0	0	1	1	3	1	2	8	3	9	4	5	9	3	1	2	13	4	0	0	0	0
	6/6	Stac.	0	0	0	0	0	1	0	3	0	11	17	6	6	5	0	0	0	1	4	0	0	0	0	0
		Grnt.	0	0	0	0	0	0	0	0	0	4	1	1	4	0	0	0	0	0	1	0	0	0	0	0
		Knck.	0	0	0	2	26	34	64	22	29	39	73	69	38	55	55	35	23	25	26	1	0	0	0	0
		Grwl.	0	0	0	1	13	7	8	7	3	11	8	7	15	13	11	8	10	8	5	0	0	0	0	0
	6/23	Stac.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	1	0	0	0	0	0	0
		Grnt.	0	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0
		Knck.	0	0	1	7	31	27	28	3	13	12	28	39	26	31	28	19	36	38	22	2	2	0	0	0
		Grwl.	0	0	0	0	5	1	2	3	3	6	5	2	2	2	4	1	8	1	4	0	0	0	0	0
	7/18	Stac.												4	3	2	8	4	0	0	1	0				
		Grnt.												4	10	6	5	9	2	3	6	0				
		Knck.												28	36	27	22	25	28	37	30	4				
		Grwl.												1	10	0	3	3	6	4	3	0				
Locomotory activity (three fish)	2/23	Fish 1	65	71	58	80	69	39	34	0	0	0	0	0	0	0	0	0	0	0	29	21	32	55	54	54
	3/25	Fish 2	31	27	44	62	44	75	25	17	4	3	2	6	1	6	2	9	0	0	14	16	17	17	29	18
			15	15	9	18	19	25	6	10	10	17	6	3	6	5	8	9	11	10	22	40	17	12	28	69
			93	85	94	40	26	28	17	9	9	1	1	1	0	1	1	0	4	5	54	68	54			
	4/15	Fish 3	23	27	17	29	38	37	22	15	8	6	6	10	7	6	9	0	2	3	17	17	22	35	51	60
			53	33	65	59	61	28	15	35	27	20	17	30	22	18	17	13	11	8	25	51	39	49	62	36
			36	55	61	59	32	5	8	6																

* Sunrise and sunset, July 1, 1965, at Oahu, Hawaii, were 5:53 AM and 7:18 PM, respectively.
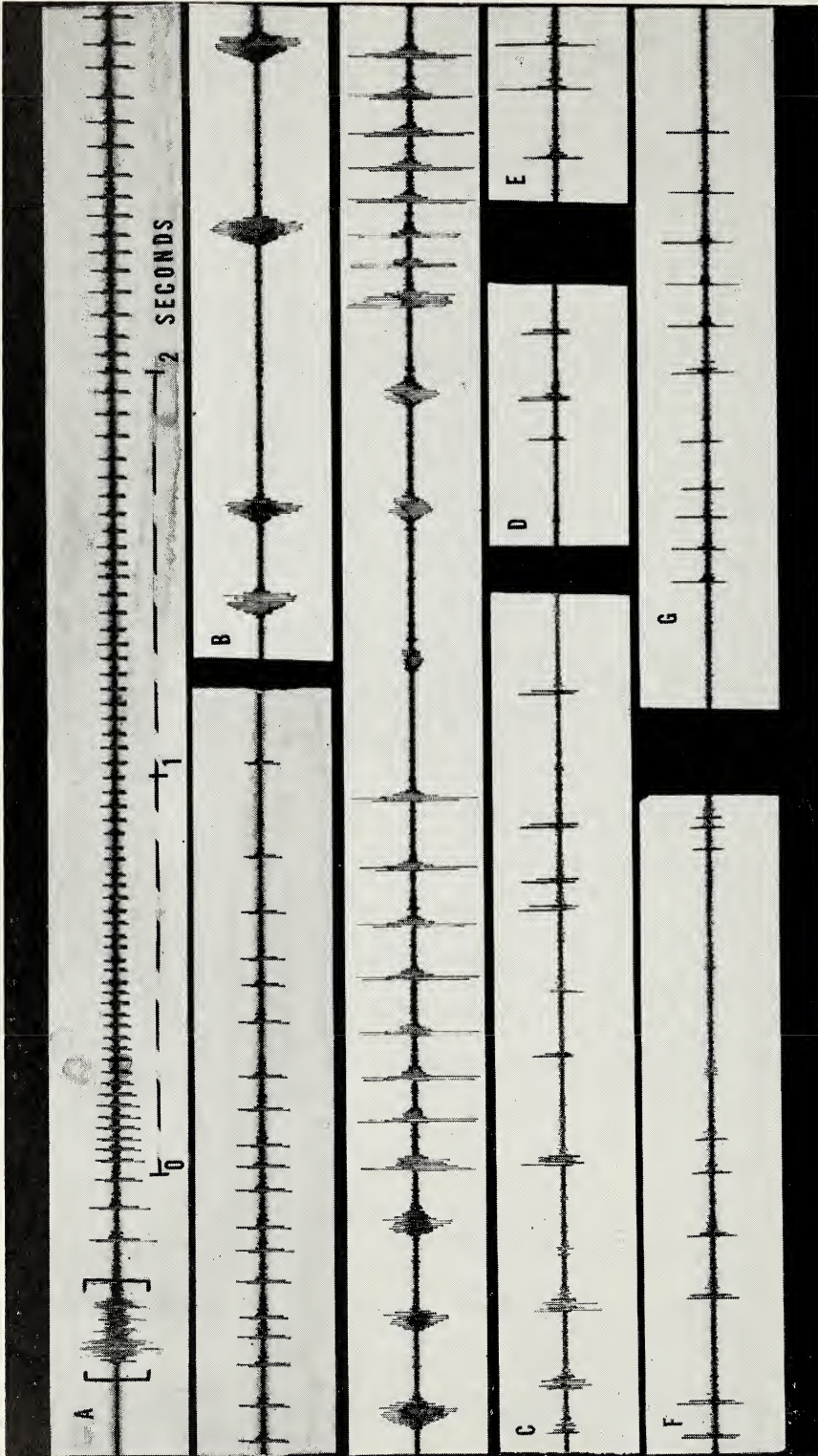
FIG. 4. Oscillographs of the four types of sounds produced by *Myripristis berndti* in the field. *A*, growl, preceded by nipping sounds (between brackets) extending through upper line to half of line 2; *B*, seven grunts, followed by a staccato, 3 grunts, and another staccato. These sounds were produced by several fish. *C–G*, Five series of knock sounds produced during separate chasing episodes between pairs of fish.

made for 1–3-hour periods. The majority of the sounds produced were staccatos and grunts. Within 1 hour after the lights were turned off, all fish had assumed a pale red color, typical of individuals caught by fishing at night in the field.

Over 90% of all aggressive interactions consisted of brief chasing (1–3 seconds), usually accompanied by knock sounds. In a few cases physical contact between the aggressive and fleeing fish occurred. In five such instances the aggressive fish produced growl sounds just after nipping took place. On these occasions the attacked fish was about the same size as the aggressor and did not flee. The oscillograph in Figure 4 illustrates a typical growl sequence. The impact sound caused by body contact between two fish (within brackets) preceded the growl by several milliseconds. In four other observations, nipping did not occur but one aggressive fish dashed rapidly toward another, stopping just short of contact, and then produced the sound with his opercula slightly extended and mouth open. Aggressive behavior infrequently involved two fish which assumed parallel head-to-tail or head-to-head positions and slowly circled, beating their tails toward one another as they rotated, with opercula and mouth open but only the caudal fins spread. Knocking sounds were produced after one fish broke away and was chased by the other.

Usually it was not possible to determine which of the two fish produced the knock sounds during a chasing episode. In cases where the aggressor chased a fish from the front to the rear of the cave, both fish involved had their heads facing away and opening of the mouth and opercula, associated with sound production, could not be observed. When chasing across the front of the cave took place, the aggressive fish often stopped swimming near the hydrophone while the fleeing fish continued moving across the front or into the cave. In such cases, knock sounds increased in intensity as the aggressive fish approached the hydrophone while the fleeing fish moved several centimeters away. Often another faint series of knocking sounds occurred just after those of the attacking fish. These differed in pitch from those of the aggressive fish, indicating that the

chased fish might also be producing sounds. The general impression (not documented) was that more sounds were produced during longer periods of chasing. The majority of all aggressive interactions were initiated by a larger fish. A summary of the aggressive interactions of all populations is shown in Table 5.

Several of the smaller fish in three populations often adopted a characteristic posture when approached by an aggressive and larger fish. They elevated their heads while simultaneously tilting the ventral region toward the aggressor, exposing the pectoral area. In all cases, the aggressive fish broke off further contact and moved away. No staccato or grunt sounds were emitted during any aggressive interactions.

Locomotory Activity of Individual Fish

The number of pen deflections caused by single fish in the activity chamber were tallied per hour (Table 4). All fish showed consistently greater locomotory activity at night from 1900 to 0800 hours. Two fish showed continued activity through 0900. There were individual differences in the degree of daytime activity. There appeared to be a gradual rise to peak nocturnal activity during the first 3 hours after midnight.

Response to Introductions of Other Fish

The number of grunt and staccato sounds produced by populations 1 minute after other fish were introduced is shown in Table 6. In no case did these sounds precede the introduction. A few grunts and one staccato sound were produced by three populations to one *H. xantherythrus, P. meeki,* and *P. porphyreus.* In all cases, introduced fish immediately entered the cave. The greatest number of sounds was produced when a moray eel was presented. After entering the cave the eel immediately curled around one of the blocks with its head protruding inside and its tail outside the cave, and remained motionless. The majority of staccato sounds were produced when the eel appeared initially, but grunts were produced throughout the 1-minute period. Other behavior by menpachi in addition to sound production consisted of orientation to the eel's head and rapid swimming movements inside the

TABLE 5

SUMMARY OF AGGRESSIVE BEHAVIOR AND ASSOCIATED SOUND PRODUCTION IN EIGHT
LABORATORY POPULATIONS OF *Myripristis berndti*

POPULATION NUMBER	DURATION OF RECORDINGS	NUMBER OF AGGRESSIVE INTERACTIONS	AGGRESSIVE FISH		AGGRESSIVE BEHAVIOR WITH:		
			LARGER	SMALLER	KNOCKS	GROWLS	NO SOUNDS
1	2 hours	31	23	8	24	3	6
2	3 hours	28	(no data)		19	0	9
3	4 hours	95	82	13	77	0	18
4	3 hours	51	35	15	36	1	14
5	1 hour	9	(no data)		5	0	4
6	3 hours	34	26	8	19	1	14
7	3 hours	29	22	7	18	2	9
8	2 hours	20	19	1	9	2	11

cave. Some fish swam to the outside and briefly "investigated" the eel's tail, then dashed back into the cave. There was no indication of mobbing or aggressiveness toward the eel.

Response to Sound Playbacks

The number of fish on each side of the tank during sound-playback experiments is shown in Table 7. When sounds were not emitted, the fish distributed themselves throughout the area under the cave. In some instances the school tended to aggregate briefly on one or the other side of the cave during the experiment. This distribution continued when background noise inherent in all playbacks and knocking sounds were played back through one of the two speakers. A few fish briefly turned toward the experimental speaker during playbacks of knocking sounds. The response to a series of staccato and grunt sounds involved several behavior patterns. Initially, all fish immediately turned to the sound source. Within 5–10 seconds, they swam toward the speaker from

which the sounds were being emitted. From 2 to 5 fish moved out of the cave to this speaker and dashed rapidly back into the cave. There was a general increase in rate of swimming movements. No staccato or grunt sounds were produced by the populations during any playbacks. The response of one population to a single staccato sound, repeated every 11 seconds during minutes 2 and 4, was comparable to responses by other fish to a series of staccato sounds. A second population tested showed a less intense response although several individuals oriented and moved toward the sound source.

DISCUSSION

The ablation experiments demonstrated that sounds were produced by a pair of bilateral muscles and the air bladder. Removal of one of the muscles reduced sound pressures, particularly in the lower frequencies (75–150 cps). The interpulse intervals and mean number of pulses per sound were comparable in

TABLE 6

NUMBER OF GRUNT-STACCATO SOUNDS PRODUCED BY LABORATORY POPULATIONS OF
Myripristis berndti ONE MINUTE AFTER INTRODUCTIONS OF OTHER FISH

INTRODUCED FISH	POPULATION NUMBER						
	1	2	3	4	5	6	7
Holocentrus xantherythrus			0–0	0–0	0–0	0–0	3–1
Priacanthus meeki			6–0	7–0	0–0	0–0	0–0
Myripristis berndti			0–0	0–0	0–0	0–0	0–0
Myripristis argyromus			0–0	0–0	0–0	0–0	0–0
Parupeneus porphyreus			0–0	1–0	0–0	0–0	0–0
Gymnothorax undulatus	32–16	19–8	80–21	36–20	78–18	43–28	115–25

TABLE 7
RESPONSE OF FOUR POPULATIONS OF *Myripristis berndti* TO SOUND PLAYBACKS*

SOUND PLAYBACK	POPULATION NUMBER	SOUND OFF		SOUND ON	
		LEFT SIDE	RIGHT SIDE	CONTROL SIDE	EXPTL. SIDE
	4	34	38	22	26
Background	5	38	46	29	27
Noise	6	34	50	33	23
	7	35	37	22	26
Many	4	39	33	3	45
Staccato	5	39	45	11	45
Sounds	6	40	44	5	51
	7	27	45	3	45
Many	4	38	34	5	43
Grunt	5	40	44	16	30
Sounds	6	54	30	4	52
	7	39	33	6	42
Single Series	4	32	40	24	24
of Knocks	5	37	47	24	32
Single Staccato	6	36	48	20	36
Sound	7	33	39	7	41

* Values represent the total number of fish on each side of the tank every 15 seconds during minutes 1, 3, and 5 when no sounds were played back, and during minutes 2 and 4 when sounds were emitted from one (experimental) side of the cave.

sounds produced by fish before and after one muscle was removed. The two bilateral muscles must then contract synchronously. The same results were obtained by Winn and Marshall (1963) with *Holocentrus rufus*. It may be that synchronous contractions of muscles associated with sound production are universal, but more evidence is needed.

The relationship between the contraction rate of sound-producing muscles and the resultant frequencies of the sounds have been investigated electrophysiologically in a few fish. Potentials recorded from *Myripristis berndti* in this study and from *H. rufus* (Winn and Marshall, 1963) corresponded in temporal relations to the pulses of sounds made by hand-held fish. Similar results have been obtained in the pigfish, *Congiopodus leucopoecilis* (Packard, 1960), the sculpin, *Myoxocephalus octodecimspinosus* (Barber and Mowbray, 1956), and for several species of catfishes (Tavolga, 1962). In squirrelfishes, handheld sounds contain frequencies from below 75 to about 4,800 cps. The fundamental frequency of the sounds (about 85 cps) is believed to be a direct translation of the muscle contraction frequency (Tavolga, 1964), while the higher frequencies are harmonics resulting

from resonance of the air bladder. It would be expected that removal of one sound-producing muscle would reduce the intensity of all frequencies, particularly the 75–150 cps octave band containing the fundamental, as was the case in *M. berndti*.

Replacing some of the gas in the air bladder with water reduced sound intensities, and when all the gas was removed, no audible sounds were produced. The results indicated that the air bladder acted as a resonator in the production of sounds. Similar results were obtained with *H. rufus* (Winn and Marshall, 1963) and other fishes in which an air bladder-muscle mechanism was involved in sound production (Tower, 1908; Hazlett and Winn, 1962).

Field observations during the day, 24-hour tape recordings, the behavior of populations in laboratory tanks, and locomotory patterns of single fish in the activity chamber lead to the following conclusions. Schools of menpachi congregate in areas of suitable cover during the day. Their presence can be detected during these times by the production of four distinct types of sounds. Fish can be caught by hook and line for a brief period after sunset (1930–2030 hours) as they emerge to leave the area.

No fish were caught within a 3-hour period after 2030, indicating that they scatter to feed some distance away from their daytime haunts, perhaps as far as adjacent sandy areas as described by Hiatt and Strasburg (1960). Few if any sounds were recorded from the area after the school had left and until it returned shortly before dawn, although the fish did produce sounds at night when confined in aquaria. Nocturnal activity of laboratory populations was similar to that of fish in the field, i.e., they began to swim more actively out of the cave and showed color changes typical of specimens caught by hook and line at night. The period of nocturnal feeding corresponded to the time of greatest locomotory activity by isolated fish in the activity chamber, as was the case with *H. rufus* (Winn et al., 1964).

Differences in behavior between *H. rufus* and *M. berndti* were observed in (1) the types of sounds produced and in their diel distribution, (2) responses of laboratory populations to sound playbacks, and (3) movements in the field. It is possible to explain these differences by comparing their nonreproductive social organization.

Individuals of *H. rufus* are territorial, but fish may maintain territories a few meters apart and certainly within acoustic range. These fish produce at least three different types of sounds: hand-held sounds, which presumably communicate the presence of a predator by a captured fish; staccatos, emitted by individuals when startled or when a predator approaches; and grunts, produced during territorial defense, especially involving intraspecific aggression but also the chasing of a nonpredatory fish of another species from the territory. Display behavior, involving fin erection, nipping, shuddering, and lateral displays are additional components of territorial defense. "Mobbing" may occur, at least under laboratory conditions, when a predator swims through closely spaced territories of a number of fish. Winn et al. (1964) have pointed out the similarity between elements of the acoustical system of *H. rufus* and certain behavior patterns of birds which roost together though maintaining territories, and which will mob a predator, show crepuscular peaks of sound production, and have analogous behavioral responses to alarm calls. The acous-

tical system of *H. rufus* aids in maintaining territories by individual fish and also promotes the survival of all fish in adjacent areas with a warning call. The peaks in production of staccato sounds at dawn and dusk are believed to be the response of territorial squirrelfish to movements of other species through their territories. The initial response of laboratory populations to playbacks of staccato sounds consisted of retreat by each individual into the open can within his territory, followed immediately after the playback by orientation to and investigation of the sound source by a few fish.

The evidence presented here indicates that *M. berndti* is nonterritorial. Fish in the laboratory were never observed to defend particular areas of the cave from others. The presence of large groups of fishes in the field, schooling under broad ledges or inside open caves, supports the contention that menpachi live in nonterritorial aggregations during the day. Further evidence was the absence of any aggressive behavior or associated sound production toward individuals of other species of nonpredatory fishes introduced to populations in the laboratory, or to diurnally active groups of reef fishes frequently observed to enter and leave habitats occupied by menpachi in the field. The presence of appeasement postures, shown by several fish in three populations, could be expected in this type of a social system. Lastly, nocturnal scattering, probably some distance from their daytime haunts, would make territoriality a highly transitory phenomenon.

The most common type of sound produced by menpachi was a series of knocks. It is assumed that these sounds are associated with the chasing of a small fish by a larger one in field populations, because only under these circumstances were the sounds produced in the laboratory. The hypothesis presented here is that, while territoriality promotes spacing of individuals in *H. rufus,* chasing and knock sounds function to maintain distance between individuals in *M. berndti.* This does not mean that some fish would be driven into open water, but that they would tend to space themselves throughout a given cave or ledge area, reducing the danger that more than one individual could be caught by a predator and increasing the likelihood that a predator approaching from

any direction would be detected. Moray eels were prominent potential predators, often seen in pairs or larger aggregations in the same habitat as menpachi.

Growl sounds produced in the laboratory were associated with more intense aggressive interactions. This sound is associated with aggressiveness between pairs of fish both willing to fight. In about half the observed cases these sounds followed nipping between the two fish. When one of the two fish fled, knocks were produced by the attacking fish and, possibly, also by the fleeing fish.

In three of the four field recordings, there was no evidence of a crepuscular peak in the production of staccato and grunt sounds. In one recording, a dusk peak occurred (April 28–29). This was the only case when the hydrophone cable was not secured near the surface with an air-filled bottle. Movements of the loose cable on the bottom under the ledge, combined with decreased light intensities, may have been responsible for the production of these sounds.

The response of laboratory populations to moray eels consisted of orientation to the eel's head, investigation of its tail, increase in rate of swimming movements, and the production of many grunt and a few staccato sounds. The response of natural populations to a diver was similar acoustically, but the fish had room to escape by scattering to either side or back into darker recesses. More staccato sounds were produced by laboratory populations during the first few seconds after the eel appeared, while grunts were produced throughout the 1-minute recording period, though at a decreasing rate as time passed and the eel made no further movement after entering the cave. Apparently the tendency to produce grunt sounds habituates at a slower rate than staccatos. Probably staccatos represent the most intense warning response to danger stimuli. These sounds were also occasionally produced by startled menpachi during introductions of nonpredatory fish which suddenly entered the cave.

Sound-playback experiments to four laboratory populations indicated that fish responded differently to various types of their own sounds. There was no observable change in the behavior of fish during playbacks of background

sounds. Some fish oriented to the speaker when knocking sounds were played back, but did not move to the sound source. The response to playbacks of both staccato and grunt sounds involved immediate orientation, followed by movements toward the sound source. Playbacks of staccato sounds suppressed activity in *H. rufus,* i.e., the fish retreated into their cans during the playback, as would be expected when the territory also included a protective area. Orientation to the sound source occurred just outside the can and, in some cases, the fish moved toward and investigated the experimental speaker after the sound had been turned off. These differences in responses by both species to their warning sounds can be attributed to territoriality in *H. rufus* and its absence in menpachi. In both cases it is clear that *M. berndti,* and probably *H. rufus,* are capable of orienting to a sound source located a few meters away, and that staccatos (and grunts in menpachi) warn that a predator is present and also indicate his location. A warning sound with no directional information would be of limited use when large numbers of fish are aggregated in areas of low light intensity, probably not alone sufficient to permit visual localization of a well camouflaged predator. Presumably, the responses in the laboratory are made to the "near field" components of the sounds, since they occur within a meter of the source. The results support van Bergeijk's (1964) contention that fishes are capable of localizing sounds within the near field. It would seem that *M. berndti,* which shows such clear responses to some playbacks, would be a good species to test for sound localization at greater distances in the far field.

Reproductive activities in fish have led to the evolution of one or, usually, two distinct types of sounds. One of these, usually produced by males, presumably attracts and/or sexually stimulates the female. Some examples are the "boat-whistles" of toadfish (Gray and Winn, 1961; Winn, 1964), "purrs" of *Notropis analostanus* (Stout, 1963), and the sounds of male *Bathygobius soporator* and *Chasmodes bosquianus* (Tavolga, 1956, 1958). The same sound may function in aggressive interactions between males during the breeding season, as in the cod (Brawn, 1961), but often a second

sound is used in nest defence or male-male fighting, for example the "knocks" of *N. analostanus,* and grunts and growls of toadfish and midshipman (Gray and Winn, 1961; Cohen and Winn, in preparation). In *M. berndti,* an acoustical system involving the production of at least five types of sounds, including the hand-held grunt, has been evolved. These sounds are correlated with nonreproductive behavior patterns. Other sounds may be used during spawning, but to date no information is available. It may be supposed that the development of increasingly complex acoustical systems (more distinct types of sounds correlated with specific behaviors or with different intensities of one behavior pattern) will occur when large numbers of fishes aggregate throughout the year, at least for certain periods of the day. Such aggregations promote a variety of intraspecific contacts in different behavioral contexts and increase problems of vulnerability to predators. This explanation might account for two types of sounds associated with different intensities of aggressive behavior (knocks and growls) and warning (staccatos and grunts) in *M. berndti.* There have been few studies to date, but it is interesting that several (3–5) types of sounds have been recorded from nonreproductive groups of squirrelfishes and aggregations of marine catfishes (Tavolga, 1960).

Winn (1964) has proposed that fish sounds may be categorized into five basic types: variable interval, fixed interval, unit duration, time-length, and harmonic-frequency signals. Intermediates are not uncommon. He has suggested that information could be transmitted by varying the intervals as well as the unit lengths, although there are cases when these variables do not seem to be involved. Differences in intervals and duration of units appear to differentiate sounds produced by menpachi, although there are also some minor differences in frequency and intensity between various sounds. Since *M. berndti* responds preferentially to some of its own signals, it might be possible to test these variables with artificial sound playbacks. It is assumed that all types of sounds in these fish are produced by different temporal patterning of contractions by the same pair of muscles associated with the air bladder.

The squirrelfish are well suited for bio-

acoustical studies because they will produce sounds and can usually be kept under seminatural conditions in the laboratory for observations and experiments. At least two other species in the Hawaiian area (*Holocentrus xantherythrus* and *H. lacteoguttatus*) produce different sounds in intraspecific aggressive behavior and warning (Salmon, unpublished observations). While *H. xantherythrus* was found in groups under ledges and in caves, *H. lacteoguttatus* appeared to be territorial. It appears that quite different types of social organization and patterning of sounds may be characteristic of each species of squirrelfish. Further studies on other species may yield valuable information on the evolutionary development of acoustical communication in the Holocentridae, and in marine fishes in general.

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The Ecology of Pelagic Amphipoda, I

Species Accounts, Vertical Zonation and Migration of Amphipoda from the Waters off Southern California

Gary J. Brusca[1]

A series of midwater trawls in the waters off the coast of southern California has revealed large numbers of pelagic amphipods. A sampling program employing an Issacs-Kidd Midwater Trawl (Issacs and Kidd, 1953: 1–21) was conducted in the waters of the Outer Santa Barbara Passage, in the area of the Santa Catalina Basin.

The purposes of this study were (1) to determine the constituents of the local pelagic amphipod fauna, (2) to examine the vertical distributional and migrational patterns of the abundant species, and (3) to analyze some of the hydrographic conditions of the study area and relate this information to the ecology of the amphipods.

This is the first in a planned series of papers. In view of the forthcoming works, such data as size distributions, reproductive conditions, and density fluctuations are omitted from this present paper.

All of the collections considered in this study were obtained through the use of the R/V "Velero IV" of the Allan Hancock Foundation, University of Southern California. Partial support for this work was furnished by grants from the National Science Foundation (G-10691 and G-23467).

METHODS AND MATERIALS

An Issacs-Kidd Midwater Trawl (IKMWT) with a 10×10-ft fishing aperture was used in all collections discussed here. A few samples were taken with a Foxton closing device attached to the IKMWT. The Foxton device not only takes a sample at a prescribed fishing depth but retains, separately, the material col-

lected as the trawl is being lowered and raised. Only partial success was attained with this device.

Horizontal tows were taken, and fishing depths were determined through the use of a pressure depth gauge and by triangulation. Although these two methods yielded comparable measurements, the fishing depths recorded here may present some error. The pressure gauge records only the greatest depth to which the trawl descends, and it is the opinion of this author and other workers (Aron et al., 1964:324–333) that the fishing depth of the IKMWT fluctuates while it is being towed. Most of the trawls were conducted for 2-hour periods.

Of the 82 samples used in this study, 58 were quantitatively analyzed by converting counts made in pint aliquots to numbers per hour trawling time. Total counts presented in this paper indicate the number of individuals sorted from these pint aliquots. Although the recorded numbers per trawl hour probably are not precise, they are used at times to offer comparative values of relative population densities at various depths. The qualitative samples were used to determine presence or absence of species at particular times and depths. Table 1 is a record of the day and night hauls taken at various depths. Complete station data and individual sample analyses are on file with the author.

HYDROGRAPHY OF THE STUDY AREA

The continental shelf off the coast of southern California is a complex series of basins, troughs, and islands. It has been termed a continental borderland (Shepard and Emery, 1941:9) due to the striking differences between its topography and that of typical shelf areas. Emery (1960:32–61) offered a detailed description of this region.

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TABLE 1

Depth Distribution of Day and Night Samples Taken in the Outer Santa Barbara Passage

DEPTH IN METERS	NO. QUANTI- TATIVE SAMPLES	NO. QUALI- TATIVE SAMPLES	TOTAL NO. SAMPLES
Night			
0–50	2	2	4
50–100	2	0	2
100–200	5	2	7
200–300	3	1	4
300–400	4	2	6
400–500	2	0	2
500–600	4	3	7
600–700	2	0	2
700–800	1	0	1
800–900	0	1	1
900–1100	1	2	3
Day			
0–50	0	2	2
50–100	0	2	2
100–200	0	2	2
200–300	3	1	4
300–400	3	1	4
400–500	4	1	5
500–600	5	0	5
600–700	3	1	4
700–800	3	0	3
800–900	4	0	4
900–1100	7	1	8

Certain hydrographic data were utilized in determining the effects of oceanographic conditions on the habits of the pelagic amphipods. Some of this information was obtained from data collected from four stations in the Outer Santa Barbara Passage occupied by the California Cooperative Fisheries Investigations (CCOFI) research vessel. In addition to the CCOFI reports, several bathythermograph readings were taken from the "Velero IV" at times of biological collecting.

From the information gathered, Table 2 was constructed to illustrate the variation in thermocline depth and intensity throughout the year.

Although fluctuations in surface water salinities were noted in the CCOFI reports, there was no indication that the halocline had any effect on the vertical distribution of the amphipods.

The identification of water masses off the southern California coast is difficult due to the

great amount of mixing and the formation of complex eddy systems as the California Current passes Point Conception. Emery (1960: 97–115) presented a description of the currents of the local shelf waters and suggested that a zone of mixing between the northern water of the California Current and a deeper layer of southern water exists at depths of from 200 to 300 m. Analysis of temperature-salinity diagrams drawn from the CCOFI data suggests the possibility that the water of the Outer Santa Barbara Passage below about 100 m is an area of mixing of east and west North Central Pacific water. In some cases T-S values approach readings indicative of Pacific equatorial water. These measurements may reflect the incorporation of southern water as the eddy systems turn northward below Point Conception. The surface waters are subject to a great deal of seasonal variation, especially in temperature. The surface salinity values (above 100 m) are typical of those reported as Pacific subarctic water. This top 100 m may be subarctic water which has been heated by solar radiation with very little salinity change as it is brought into lower latitudes by the California Current.

SPECIES ACCOUNTS

Suborder GAMMARIDEA

Family EUSIRIDAE

Rhachotropis natator (Holmes)

Gracilipes natator Holmes, 1908: 527–529, figs. 32–34; Thorsteinson, 1941: 85, pl. 6, figs. 67–70.

Rhachotropis natator Barnard, J. L., 1954a: 54–56, pl. 6.

This species occurred in 15 samples taken in this study at depths of 600 to 1100 m. A total of 77 individuals was recorded in quantitative samples. Table 3 illustrates the day and night distributions of this species and shows some evidence of vertical movement. The population appeared to be of about uniform density during the daylight hours between 600 and 1100 m, but during the night captures were made only at depths greater than 900 m. Indicated here is a movement into shallower water dur-

TABLE 2

General Seasonal Variations in Surface Temperature and Thermocline Depth and Intensity in the Outer Santa Barbara Passage

MONTH	SURFACE T°C	DEPTH OF THERMOCLINE MIDPOINT	T°C CHANGE IN TOP 40 METERS
January	14.00	absent	less than 1
February	13.80	absent	less than 1
March	14.50	20 m	3.0
April	14.00	15 m	3.0
May	17.50	25 m	4.5
June	18.00	20 m	5.0
July	19.00	no data	no data
August	21.00	18 m	8.3
September	21.10	27 m	5.1
October	20.10	25 m	4.0
November	16.85	25 m	5.3
December	15.00	absent	1.3

ing the day. The factors influencing this type of deep-water migration are not clear. The absence of perceivable light and the relative constancy of temperatures exclude these factors as being important at such great depths. The vertical movement of *Rhachotropis natator* may, in fact, represent an endogenous rhythm and thus be independent of the environmental conditions.

Family LYSIANASSIDAE

Eurythenes obesus (Chevreux)

Katius obesus Chevreux, 1905: 1–5, figs. 1–3; Stephensen, 1925: 126–127; Schellenberg, 1926: 217–218, fig. 26*d*; Barnard, K. H., 1932: 56–58, fig. 21, pl. 1, fig. 1; Chevreux, 1935: 63–65, pl. 10, figs. 4–6, pl. 11, fig. 10.

TABLE 3

Day and Night Depth Distributions for *Rhachotropis natator*

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
600–900	4	0	0
900–1100	3	3	100
Day			
600–900	11	6	54.5
900–1100	8	6	75

Eurythenes obesus Shoemaker, 1956: 177–178; Barnard, J. L., 1961: 38–39, fig. 8.

A total of 6 specimens of this species was recovered from 5 samples ranging in depth from 685 to 1000 m. The possibility of demersal activity was suggested by Barnard (1961: 26). He reported that *Eurythenes obesus* had been taken in both pelagic and benthic samples, stipulating the possibility of benthic gear capturing pelagic organisms. The individuals recovered in this present study were certainly many meters above the bottom. Gut analyses revealed debris and what appeared to be silicious sponge spicules which may indicate benthic feeding. If this species does feed on the bottom it must migrate vertically some 500 to 600 m, as indicated by the capture depths and the fact that the floor of the Santa Catalina Basin is at a depth of 1436 m.

Paracallisoma coecus (Holmes)

Scopelocheirus coecus Holmes, 1908: 500–502, figs. 10–12; Barnard, J. L., 1954*a*: 54, pls. 4–5.
Paracallisoma coecus Barnard, J. L., 1954*b*: 57.

This species, known only from the waters off the coast of southern California, occurred in 14 samples from depths ranging from 520 to 1100 m. A total of 56 individuals was recovered from quantitative samples. J. L. Bar-

TABLE 4

Day and Night Depth Distributions for
Paracallisoma coecus

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
500–900	11	2	18
900–1100	3	2	66
Day			
500–900	16	4	25
900–1100	8	6	75

nard (1954a:54) reported a depth-range of
from 654 to 1,030 fathoms (1196 to 1884 m)
for this species. All of the individuals collected in this present study were from shallower
depths (520–1100 m).

Some evidence exists that *Paracallisoma coecus* moves upward during the daylight hours.
Table 4 shows that the relative abundance of
this species was greater during the daytime,
suggesting that some of the population was
residing at depths greater than those sampled
during this study. This suggestion is also supported by the depth records stated by Barnard.

This species was scarce from depths of less
than 900 m. The average number per trawl
hour in the five positive samples from depths
less than 900 m was 5, while this value for
the nine positive samples taken deeper than
900 m was 36.

Cyphocaris anonyx Boeck

Cyphocaris micrononyx Stebbing, 1888: 656,
pl. 16.
Cyphocaris anonyx Boeck, 1871: 104–105;
Schellenberg, 1926: 210–212, figs. 2b, 5a–b,
pl. 5, fig. 2; Shoemaker, 1945: 187, figs. 1a–b;
Barnard, J. L., 1954a: 53; Waterman, 1939:
256–279.

A total of 115 individuals was recovered
from quantitative samples during this study.
Shoemaker (1945:187) recorded this species
at depths of from 600 to 1,000 fathoms (1161
to 1935 m), and a single specimen was reported by J. L. Barnard (1954a:53) taken in
a net tow from 560 to 640 fathoms (1084 to
1239 m). Waterman et al. (1939:268) re-

ported *Cyphocaris anonyx* taken at depths of
from about 200 to 1000 m. This present study
revealed individuals of this species in 27 samples at depths of from 150 to 1100 m. Waterman also recorded a large portion of the population moving from 600 m in the daytime to
about 200 m at night. Some evidence for this
migration is found in the capture times and
depths of this present study, but it is not
conclusive.

Cyphocaris richardi Chevreux

Cyphocaris Richardi Chevreux, 1905: 1–5,
figs. 1–2; Chevreux, 1916:1.
Cyphocaris richardi Schellenberg, 1926:206–
209, figs. 2a, 3a–e, 4a–d, pl. 5, fig. 1; Barnard,
K. H., 1932:35; Stephensen, 1933:4–5; Shoemaker, 1945:187–189, fig. 1d; Barnard, J. L.,
1954a:54, pls. 2–3; Barnard, J. L., 1961:32;
Barnard, J. L., 1962:24; Bernstein and Vinogradov, 1955:212–213, figs. 2–3; Bernstein and
Vinogradov, 1958:221.

Collected in 28 trawls, a total of 193 individuals was taken in quantitative aliquots.
Positive samples ranged in depth from 500 to
1100 m. Table 5 illustrates the day and night
depth distributions for *Cyphocaris richardi*.
From these data it can be seen that this species
was rather evenly distributed between 500 m
and the depth of the deepest samples taken
(1100 m). There is no conclusive evidence
of any vertical movement.

Suborder HYPERIIDEA

Family PLATYSCELIDAE

Platyscelus serratulus Stebbing

Platyscelus serratulus Stebbing, 1888:1470;
Stephensen, 1925:215–218, chart 31; Chevreux and Fage, 1925:422, fig. 414; Barnard,
K. H., 1930:437; Pirlot, 1930:37; Barnard,
K. H., 1932:298; Shoemaker, 1945:259;
Hurley, 1956:21–22.

Platyscelus serratulus occurred in 6 samples
during this study, a total of 8 specimens was
recorded at depths ranging from 170 to 927
m. Stephensen (1925:215–218) reported finding this species at the surface at night. Although only a few individuals were taken dur-

TABLE 5

DAY AND NIGHT DEPTH DISTRIBUTIONS FOR
Cyphocaris richardi

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
500–900	11	6	55
900–1100	3	3	100
Day			
500–900	16	12	75
900–1100	8	7	88

ing this present study, there is some evidence of a vertical movement toward the surface during the dark hours. The report by Stephensen and the depth and time records presented by Hurley (1956:21–22) support this suggestion.

Family PRONOIDAE

Eupronoe minuta Claus

Eupronoe minuta Stephensen, 1925:160–161, figs. 55–56; Chevreux and Fage, 1925: 425–426, fig. 417; Pirlot, 1929:148–149; Barnard, K. H., 1930:426; Pirlot, 1930:34–35; Barnard, K. H., 1932:289; Shoemaker, 1945: 245–246; Hurley, 1956:19.

A total of 322 individuals of this species was taken from quantitative samples. It was present in 41 trawls ranging in depth from 50 to 1100 m. Table 6 illustrates the day and night depth distributions. *Eupronoe minuta* was one of the two species common at depths of less than 100 m during the daylight hours. The greatest concentrations of individuals were noted from about 50 to 200 m during the day; the rest of the population was rather evenly distributed throughout the depth range of the sampling program. The reason for the apparent absence of individuals between 400 and 500 m is not clear. The nighttime depth distribution shows an obvious massing of the population in the surface waters. Data gathered with the Foxton closing device indicate that the deep, positive, night samples are probably the result of contamination from upper layers as the net was being lowered and raised. This does not exclude the possibility, however,

that this species may descend during the dark hours.

Family PHROSINIDAE

Primno macropa Guerin

Euprimno macropa Stephensen, 1924:143–146, chart 22; Pirlot, 1929:130–131; Pirlot, 1930:22.

Primno macropa Barnard, K. H., 1930:424–425; Barnard, K. H., 1932:287–288; Thorsteinson, 1941:93–94, pl. 9, figs. 98–102; Mackintosh, 1934:90, fig. 20; Shoemaker, 1945:234–236; Hurley, 1956:17–18.

This species occurred in 40 samples ranging in depth from 80 to 980 m. A total of 315 individuals was recovered from aliquots of quantitative samples.

Mackintosh (1934:90) offered data which suggest that *Primno macropa* migrates to the surface during the daylight hours and moves

TABLE 6

DAY AND NIGHT DEPTH DISTRIBUTIONS FOR
Eupronoe minuta

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
0–50	4	1	25
50–100	2	2	100
100–200	7	4	57
200–300	4	0	0
300–400	6	4	66
400–500	2	0	0
500–600	7	0	0
600–700	2	2	100
700–800	1	0	0
800–900	1	0	0
900–1100	3	0	0
Day			
0–50	2	1	50
50–100	2	2	100
100–200	2	2	100
200–300	4	2	50
300–400	4	3	75
400–500	5	0	0
500–600	5	3	60
600–700	4	3	75
700–800	3	2	66
800–900	4	2	50
900–1100	8	5	62

deeper at night. His study was conducted in Antarctic waters. The present study, however, gives evidence that this species undergoes a typical migratory activity toward the surface at night and retreats to deeper water during the day (Table 7). The daytime depth range was from 200 to 980 m and the nighttime range was from 80 to 650 m. The deep, positive, night samples probably indicate a descent of part of the population during the dark hours.

Family CYSTISOMIDAE

Cystisoma fabricii Stebbing

Thaumatops fabricii Stephensen, 1918:63–64, figs. 22–23; Pirlot, 1929:89.
Cystisoma fabricii Stebbing, 1888:1333; Barnard, K. H., 1932:272–273; Hurley, 1956:10.

A total of 31 individuals was collected from 19 samples ranging in depth from 275 to 1100 m. There is some evidence that this species

TABLE 7

Day and Night Depth Distributions for
Primno macropa

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
0–50	4	0	0
50–100	2	2	100
100–200	7	4	57
200–300	4	1	25
300–400	6	3	50
400–500	2	2	100
500–600	7	3	43
600–700	2	2	100
700–800	1	1	100
800–900	1	0	0
900–1100	3	0	0
Day			
0–50	2	0	0
50–100	2	0	0
100–200	2	0	0
200–300	4	3	75
300–400	4	2	50
400–500	5	3	60
500–600	5	3	60
600–700	4	1	25
700–800	3	2	66
800–900	4	2	50
900–1100	8	4	50

rises toward the surface at night but this is speculative due to the small number of individuals collected.

Cystisoma pellucidum (Suhn)

Thaumatops pellucida Stephensen, 1918:64–66, figs. 19, 24–27.
Cystisoma pellucidum Barnard, K. H., 1932:272; Thorsteinson, 1941:92–93; Hurley, 1956:10.

Four individuals of this species were taken in 4 samples ranging in depth from 275 to 468 m. Although vertical movements are suspected for *Cystisoma pellucidum,* the data are too scant to support the suggestion.

Family OXYCEPHALIDAE

Calamorhynchus pellucidus Streets

Calamorhynchus rigidus Stebbing, 1888:1600, pl. 206; Bovallius, 1890:74; Stephensen, 1925:189–191.
Calamorhynchus pellucidus Streets, 1878:285, pl. 2, fig. 5; Bovallius, 1890:73–74, pl. 2, figs. 14–15; Fage, 1960:31–37, figs. 19–20.

This is the first record of this species from Pacific North America. Only 1 specimen was collected during this study, at a depth of 360 m. Although vertical migration is suspected from analysis of earlier works, no conclusions can be drawn here.

Oxycephalus clausi Bovallius

Oxycephalus clausi Bovallius, 1890:60, figs. 4, 7, 8, 22, 54, 65, pl. i, figs. 19–24, pl. ii, fig. 1; Stephensen, 1925:188, chart 27; Barnard, K. H., 1930:433; Barnard, K. H., 1932:294; Fage, 1960:20–21.

This is the first record of this species from Pacific North America. Two individuals were taken at depths of 360 and 520 m. Earlier work suggests a migration toward the surface at night.

Streetsia challengeri Stebbing

Streetsia pronoides Bovallius, 1890:34, pl. III, figs. 7–12, p. 23, fig. 9, p. 35, fig. 62; Pirlot, 1938:360; Hurley, 1956:18–19.

TABLE 8

DAY AND NIGHT DEPTH DISTRIBUTIONS FOR
Streetsia challengeri

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
0–50	4	2	50
50–100	2	2	100
100–200	7	4	59
200–300	4	2	50
300–400	6	0	0
400–500	2	0	0
500–600	7	0	0
600–700	2	1	50
700–800	1	0	0
800–900	1	1	100
900–1100	3	0	0
Day			
0–50	2	0	0
50–100	2	0	0
100–200	2	0	0
200–300	4	3	75
300–400	4	4	100
400–500	5	2	40
500–600	5	2	40
600–700	4	1	25
700–800	3	0	0
800–900	4	2	50
900–1100	8	3	37

Streetsia challengeri Stebbing, 1888:1603–1606, pl. 207; Stephensen, 1925:194–199, fig. 75; Pirlot, 1929:164–165; Barnard, K. H., 1930:435; Barnard, K. H., 1932:295; Shoemaker, 1945:255; Fage, 1960:51–63, figs. 36–43.

This species was captured in 31 trawls at depths of from 10 to 1100 m. A total of 67 individuals was sorted from pint aliquots of the quantitative samples.

There is definite evidence of diurnal migration toward the surface at night (Table 8). Results of sampling with the Foxton device indicate that the two positive, deep, nighttime samples were probably the result of contamination from shallower depths.

Family HYPERIIDAE

Hyperia spinigera Bovallius

Hyperia spinigera Barnard, K. H., 1932:273–274, fig. 160; Thorsteinson, 1941:87–88,

pl. 8, figs. 79–82; Shoemaker, 1945:238, fig. 35; Hurley, 1956:15.

Eight individuals of this species were taken in 5 samples at depths of from 300 to 954 m. Although only a few specimens were recovered, there is some evidence of vertical movement upward at night.

Hyperia bengalensis (Giles)

Hyperia bengalensis Shoemaker, 1942:49; Shoemaker, 1945:238; Hurley, 1956:15–16.

Some taxonomic confusion accompanies this species; Hurley (1956:15–16) gives an account of the systematics. The specimens collected in this present study are very similar to that pictured by Stebbing (1888) as *H. schizogeneios*.

This species was collected in 13 samples ranging in depth from 85 to 975 m. A total of 52 individuals was sorted from quantitative aliquots. There is definite evidence that *Hyperia bengalensis* moves toward the surface at night. Its daytime depth range was from 288 to 975 m, while at night it was collected from 85 to 650 m.

Hyperia galba (Montague)

Hyperia galba Sars, 1895:7, pl. 2, fig. 1; Calman, 1898:265; Stephensen, 1924:81, chart 11; Barnard, K. H., 1932:273.

Hyperia galba was collected in 31 trawls at depths of from 85 to 1100 m, and 78 individuals were taken from pint aliquots of quantitative samples.

The data shown in Table 9 indicate an obvious migration toward the surface at night, concentrating at depths of less than 500 m.

Family VIBILIIDAE

Vibilia armata Bovallius

Vibilia armata Chevreux and Fage, 1925:387–388, fig. 391; Pirlot, 1929:100–101; Pirlot, 1930:11; Barnard, K. H., 1930:104; Barnard, K. H., 1932:264–265; Hurley, 1956:10–11.

This species was found in 54 samples at depths of from 10 to 1100 m. A total of 2,742

TABLE 9

DAY AND NIGHT DEPTH DISTRIBUTIONS FOR
Hyperia galba

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
0–50	4	0	0
50–100	2	1	50
100–200	7	2	28
200–300	4	4	100
300–400	6	3	50
400–500	2	1	50
500–600	7	1	13
600–700	2	0	0
700–800	1	0	0
800–900	1	0	0
900–1100	3	0	0
Day			
0–50	2	0	0
50–100	2	0	0
100–200	2	0	0
200–300	4	1	25
300–400	4	4	100
400–500	5	2	40
500–600	5	3	60
600–700	4	0	0
700–800	3	2	75
800–900	4	1	25
900–1100	8	6	75

TABLE 10

DAY AND NIGHT DEPTH DISTRIBUTIONS FOR
Vibilia armata

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
0–50	4	3	75
50–100	2	2	100
100–200	7	5	70
200–300	4	3	75
300–400	6	5	82
400–500	2	2	100
500–600	7	2	30
600–700	2	2	50
700–800	1	1	100
800–900	1	0	0
900–1100	3	0	0
Day			
0–50	2	0	0
50–100	2	0	0
100–200	2	0	0
200–300	4	3	75
300–400	4	2	50
400–500	5	4	80
500–600	5	5	100
600–700	4	2	50
700–800	3	2	66
800–900	4	3	75
900–1100	8	7	88

individuals was noted in quantitative aliquots.

The data suggest that *Vibilia armata* exists in a thick zone ranging from the surface to about 800 m at night and from 200 to 1100 m during the day. It is probable that the lower, daytime depth limit was greater than the sampling program of this study. Table 10 illustrates the depth distributions. It appears that the entire population moves upward some 200 m at night without actually concentrating near the surface.

Vibilia viatrix Bovallius

Vibilia californica Holmes, 1908:490–492, figs. 1–2.
Vibilia viatrix Stephensen, 1918:41–43, fig. 13; Chevreux and Fage, 1925:385–386, fig. 390; Pirlot, 1929:95–96; Barnard, K. H., 1930:403; Pirlot, 1930:10–11; Barnard, K. H., 1932:262–263; Shoemaker, 1945:234, Hurley, 1956:11.

Individuals of this species were taken in 53 trawls ranging in depth from 10 to 1100 m. A total of 658 specimens was recovered from pint aliquots. A few individuals associated with salps were noted on the surface.

Table 11 illustrates the day and night depth distributions. This species displayed a unique pattern of vertical migration: the upper portions of the population remained rather stable, while the deeper dwelling members rose at night, resulting in an absence of individuals at great depths during the dark hours.

Family PHRONIMIDAE

Phronima sedentaria (Forskal)

Phronima sedentaria Holmes, 1908:490; Stephensen, 1924:114–121, figs. 50–51, chart 15; Chevreux and Fage, 1925:393–395, fig. 396; Pirlot, 1929:110–112; Barnard, K. H., 1930:422; Pirlot, 1930:12–14; Barnard, K. H.,

TABLE 11

DAY AND NIGHT DEPTH DISTRIBUTIONS FOR
Vibilia viatrix

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
0–50	4	4	100
50–100	2	1	50
100–200	7	4	57
200–300	4	3	75
300–400	6	4	66
400–500	2	2	100
500–600	7	1	14
600–700	2	2	100
700–800	1	1	100
800–900	1	0	0
900–1100	3	0	0
Day			
0–50	2	2	100
50–100	2	1	50
100–200	2	1	50
200–300	4	1	25
300–400	4	4	100
400–500	5	4	80
500–600	5	4	80
600–700	4	2	50
700–800	3	3	100
800–900	4	3	75
900–1100	8	7	87

TABLE 12

DAY AND NIGHT DEPTH DISTRIBUTIONS FOR
Phronima sedentaria

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
0–50	4	0	0
50–100	2	2	100
100–200	7	7	100
200–300	4	2	50
300–400	6	4	66
400–500	2	0	0
500–600	7	3	47
600–700	2	2	100
700–800	1	1	100
800–900	1	0	0
900–1100	3	2	75
Day			
0–50	2	0	0
50–100	2	0	0
100–200	2	0	0
200–300	4	4	100
300–400	4	4	100
400–500	5	4	80
500–600	5	4	80
600–700	4	2	50
700–800	3	2	75
800–900	4	2	50
900–1100	8	6	75

1932:283–284; Thorsteinson, 1945:236; Hurley, 1956:16.

Phronima sedentaria was collected in 53 trawls at depths of from 80 to 1100 m. A total of 575 individuals was sorted from quantitative aliquots.

During the daytime this species was found at depths ranging from about 275 to 1100 m, with the greatest concentrations noted above 400 m. There was a distinct rise of the population toward the surface at night (Table 12). The deep, positive samples at night may be the result of either a descent during the dark hours or the presence of a nonmigrating portion of the population residing below the depth of perceivable light. There is also the probability of some contamination from shallower depths.

It has been suggested in much of the earlier literature that only the young of this species were ever captured near the surface and that the adults were typically taken in deep trawls. Mean size records obtained during this present study showed no difference in age groups for individuals captured above and below a depth of 100 m.

Family PARAPHRONIMIDAE

Paraphronima gracilus Claus

Paraphronima gracilus Stephensen, 1924: 75–77; Chevreux and Fage, 1925:391, fig. 394; Pirlot, 1929:104–105; Barnard, K. H., 1932: 267; Hurley, 1956:12–13.

Paraphronima gracilus was taken in 49 trawls ranging in depth from 80 to 1100 m. A total of 472 individuals was sorted from pint aliquots.

The greatest concentrations of individuals during the daylight hours were found at depths of from 275 to 400 m. This species occurred

TABLE 13

Day and Night Depth Distributions for
Paraphronima gracilus

DEPTH IN METERS	AVERAGE NO. PER TRAWL HOUR	PER CENT POSITIVE SAMPLES
Night		
0–400	72	83
400–1100	15	37
Day		
0–400	44	38
400–1100	28	82

in a great number of samples and contamination is suspected in certain deep night trawls. Density variations, however, support evidence of an ascent toward the surface during the dark hours. Table 13 shows the average numbers per trawl-hour for the positive samples, and the percentages of positive stations at different depth ranges during the day and night.

Paraphronima crassipes Claus

Paraphronima crassipes Stephensen, 1924: 77–78; Chevreux and Fage, 1925:390–391, figs. 393–394; Pirlot, 1929:105–106; Barnard, K. H., 1930:409–410; Barnard, K. H., 1932: 267–268; Shoemaker, 1945:234; Hurley, 1956: 13.

Specimens of this species were found in 54 samples ranging in depth from 80 to 1100 m. A total of 922 individuals was sorted from pint aliquots. A movement toward the surface at night was apparent (Table 14).

SUMMARY

This study treats 5 species of the suborder

TABLE 14

Day and Night Depth Distributions for
Paraphronima crassipes

DEPTH IN METERS	PER CENT POSITIVE DAY SAMPLES	PER CENT POSITIVE NIGHT SAMPLES
0–200	0	50
200–1100	75	65

Gammaridea and 16 species of the suborder Hyperiidea collected from the waters off the coast of southern California. Two additional genera (*Scina* and *Orchomenella*) were collected, but are not discussed here because of problems in specific identification. Two species of the family Oxycephalidae (*Oxycephalus clausi* and *Calamorhynchus pellucidus*) not previously reported from California waters were taken during this study, raising the known number of local pelagic hyperiids from 43 to 45.

With the exception of *Cyphocaris anonyx*, all of the gammarids were noted to be deep-living forms common only in samples taken at depths greater than about 650 m. There appear to be diurnal movements in some species, involving a rise during the daylight hours and a sinking at night. The controlling factors here are not clear, and may involve an endogenous rhythm.

With the exception of a few species, the upper depth limit of the hyperiids was defined by the thermocline, and captures were uncommon at depths of less than 50 m. From repeated sampling and analysis of abundance, it was found that most of the hyperiids exist in a thick band down to depths greater than 1000 m during the daytime, with the greatest concentrations recorded between 200 and 600 m. Most of these species rise to shallower levels during nightly migrations toward the surface.

Although it is easy to speculate on the advantages of such vertical movements, it is very difficult to establish the actual causes. The results of this study indicate that, in addition to the barrier imposed by the thermocline, light is the most important factor influencing the migrations of the hyperiids. The controlling effect of light intensity is illustrated by the massing of populations at shallow levels during periods of dim light and by the vertical spreading-out of individuals at times of total darkness.

A great deal of work remains to be done on midwater ecology in general. The use of more refined sampling methods will enable workers to establish accurate depth distributions and will offer more precise information on the habits of vertical movements.

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The Benthic and Pelagic Habitats of the Red Crab, *Pleuroncodes planipes*

Carl M. Boyd[1]

In March 1895, several specimens of an undescribed anomuran crab were washed ashore at Monterey, California. These, along with some similar animals found in oceanic waters (24°N, 130°W), were sent to William Stimpson, who was describing the crustacean material collected by the North Pacific Exploring Expedition. Stimpson described both the Monterey and the high seas specimens as a new genus and a new species, *Pleuroncodes planipes,* assigned to the family Galatheidae (Stimpson, 1860). The "red crab" or "pelagic crab" (Fig. 1) is familiar to inhabitants of Baja California and occasionally is seen along southern California beaches, where large numbers of these animals are at times washed up and left stranded by receding tides. Their brilliant red coloration, together with their relatively large size, makes such occurrences of these animals a striking phenomenon. The present study was undertaken as an investigation into the pelagic distribution and possible benthic nature of the species; prior to this study *P. planipes* was believed to be only planktonic.

Members of the family Galatheidae are typically benthic when adult and are commonly known as "squat lobsters." Larvae of all the species are pelagic for at least a short time, and presumably the small postlarvae can alternate between the plankton and the benthos before assuming an exclusively benthic life. Two antarctic species, *Munida gregaria* (Fabricius) 1793 and *M. subrugosa* (White) 1847, may be either pelagic or benthic as adults, but are more commonly benthic (Matthews, 1932). The young of *M. gregaria*—the so-called Grimothea stage—are predominantly pelagic and have been reported on several occasions as so numerous that they color the sea bright red over large areas (Matthews, 1932; Bary, 1953). *P. planipes* probably has evolved from stock that was benthic, for of the 230 described

species in the family Galatheidae only the two species of *Munida* discussed above and *P. planipes* are ever planktonic as adults.

In the new genus Stimpson also included a Chilean species described by Milne-Edwards (1837) as *Galathea monodon,* which hence became *Pleuroncodes monodon*; these are the only two species assigned to the genus at present. Initial descriptions of the two species are quite inadequate. Milne-Edwards' description of *G. monodon* morphologically fits most of the species of *Munida,* a large genus closely related to *Pleuroncodes* and containing about 41 species; however, his figures of *G. monodon,* published in 1851, are excellent. Stimpson's description of *P. planipes* (1860) is only slightly better; he did not present any figures of the new species, which apparently was first illustrated by Schmitt (1921). Schmitt's description of *P. planipes* is the most complete to date. *P. monodon* is described by Faxon (1895) and Haig (1955). The larval stages of *P. planipes* have been described in earlier papers (Boyd, 1960; Boyd and Johnson, 1963).

A fossil specimen probably belonging to *Pleuroncodes* was found by Carl L. Hubbs, of Scripps Institution of Oceanography (Miller, 1951). This specimen was from a sea cliff of the Capistrano Formation (an Upper Miocene deposit), about 1 mile south of Capistrano Beach, Orange County, California. It is not known whether the fossil was *P. planipes,* although the specimen was found well within the present-day distributional range of the species.

Specimens of *P. planipes* freshly taken by dipnet from the ocean surface immediately settle to the bottom of a shipboard aquarium and assume a benthic existence in sharp contrast to their pelagic life of a few moments earlier. Crabs kept in laboratory aquaria for growth studies lived almost entirely as benthic animals. It was believed that the question of whether the crabs were benthic in nature could not be answered conclusively by observations

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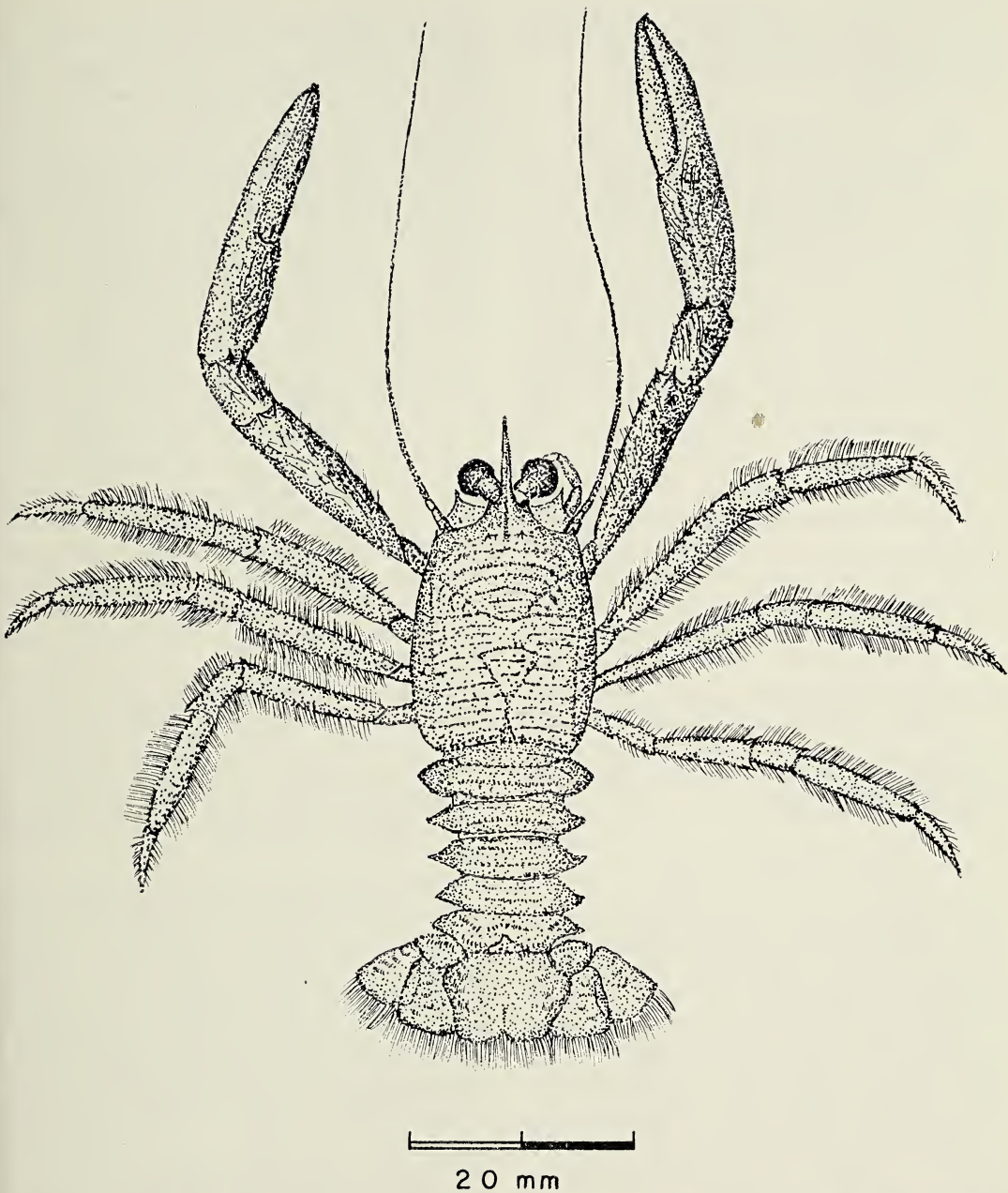
FIG. 1. Dorsal view of a male *Pleuroncodes planipes*. The standard carapace length of this specimen, as measured from the notch between the rostral and subrostral spine to the median dorsal posterior margin of the carapace was 21.3 mm. In life the abdomen is folded under the cephalothorax and the body is bright red.

in aquaria or by experimental work, but only by evidence from the field. The center of the distribution of *P. planipes* in the pelagic phase is off the western coast of southern Baja California. The bright coloration of *P. planipes*, their well-developed eyes, and the known depth distributions of other Galatheidae suggested their occurrence along the continental

shelf rather than at abyssal depths. The bottom fauna on the continental shelf of Baja California has been essentially unsampled.

METHODS

A cruise was made to the shelf area of the west coast of Baja California in the region of 26°N in November and December 1960. The following sampling and measuring devices were used at most of the stations occupied: (1) a dredge with a mouth opening 0.5 ft by 2.0 ft; this device was designed to remain closed while being raised or lowered (to avoid catching planktonic specimens), but to open upon contact with the bottom; (2) an otter trawl with a mouth 10 ft wide; (3) a series of plankton nets 1 meter in diameter which were towed horizontally, with one net close to the bottom, another intermediate in depth, and the third at the surface; the two subsurface nets were rigged with the Leavitt opening-closing device, and were open only while being towed at their specific depths; (4) a 900-ft range bathythermograph; and (5) seven Nansen bottles spaced evenly through the water column; the water from these samplers was titrated by the standard Winkler method for dissolved oxygen content.

THE BENTHIC HABITAT

On November 30, 1960 at the first station (26°02′N, 112°58′W), with a water depth of 58 fathoms, a 15-minute tow of the dredge collected 23 specimens of *P. planipes* mired in a ball of gray mud. The 10-ft otter trawl, towed on the bottom for 25 minutes at the same location, caught about 30,000 crabs. A 10-minute tow with the series of plankton nets caught one crab at the surface and none at the two lower depths. It seemed that *P. planipes* was abundant in the benthos.

During the cruise 19 one-meter net tows (each of a single net) were made at different depths at various times of day and night; 13 stations were occupied. After sampling at the first station the time of the plankton tows was lengthened to 20 minutes; each net strained about 800 m³ of water. A total of seven crabs were caught in these plankton tows. The otter

trawl, towed for 25 minutes at each station, probably strained no more than five times as much water as the meter net, but caught hundreds of crabs. The difference in catch between the plankton net and the trawl was so great it seems likely that all of the crabs caught in the otter trawl were benthic, even though the trawl remained open while it was being raised and lowered. This was substantiated by results obtained using the open-closing dredge which, with an opening only 12% of that of a meter net, caught several times as many crabs.

A transect of 5 stations was made across the continental shelf from a point 26°25′N, 112°30′W, along a course 210° true; the western-most station was 85 nautical miles from shore. The substrate on the shelf ranged from gray muddy sand to gray mud, and gave way to naked rocks with solitary corals and crinoids on the continental slope. Crabs were found abundantly on the bottom between depths of 75 and 300 m. Figure 2 presents the distribution of crabs and hydrographic data along this transect. Other stations occupied during the cruise supported the general picture. No crabs were caught on Uncle Sam Bank, which is rough and rocky, nor were any caught by trawls on subsequent cruises at the base of the continental slope in that area, at depths of 1,700 fathoms, where the sediment is again fine.

Other samples were taken on the shelf from 25°N to 31°N, but no crabs were found north of Punta San Eugenio (27°50′N). Trawls towed on a subsequent cruise in April 1961 showed the crabs to be present on the shelf at 24°N. It is probable that they occur southward to the tip of the Baja California peninsula. The benthic distribution in the Gulf of California is completely unknown, but the crabs have been seen at the surface in the Gulf and also have been washed ashore there in great numbers. It is possible that a benthic population exists in areas of the Gulf where the proper depth and substrate occur.

Considerable numbers of two other species of invertebrates were collected with *P. planipes*. One of these was the holothurian (2 cm long), *Cucumaria chilensis* Ludwig, identified by Elisabeth Deichmann of the Museum of Comparative Zoology, Cambridge, Massachusetts.

Transect heading 210°T from 26° 25'N x 112° 30' W

Transect length = 85 nautical miles
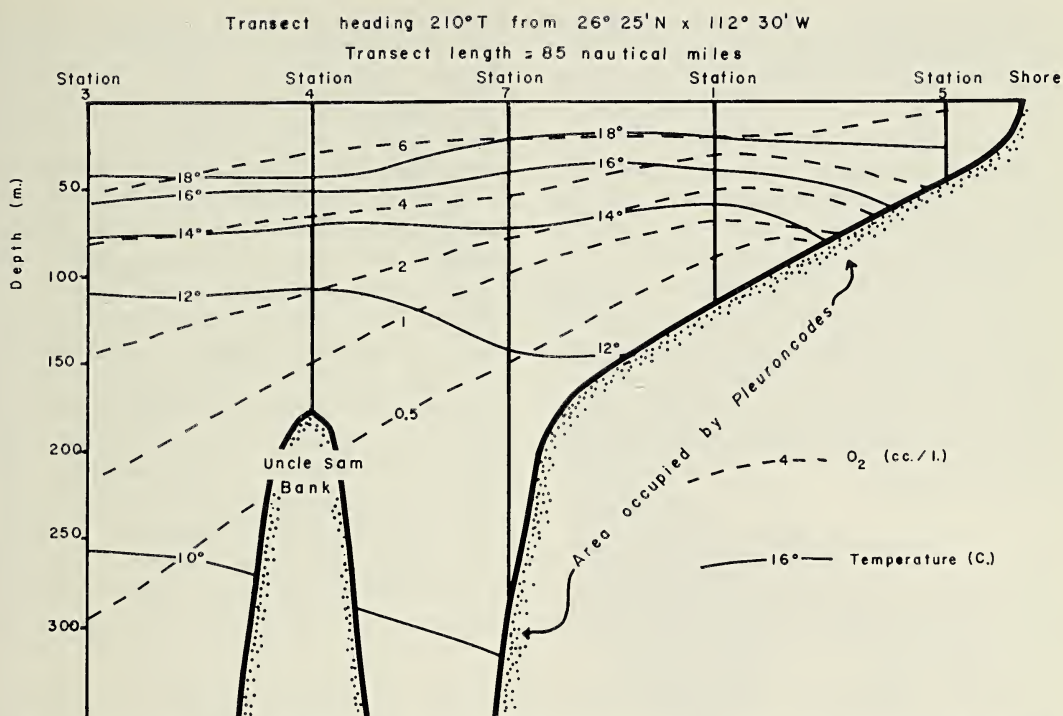
Fig. 2. Vertical profile showing bathymetry, temperature structure, oxygen concentration and distribution of *Pleuroncodes planipes* on the western coast of Baja California, Mexico, in December 1960.

P. planipes, a voracious omnivore, did not eat the holothurians when placed with them in shipboard aquaria (although the crabs would eat pieces of fish under similar circumstances). The other abundant invertebrate was a gastropod, *Nassarius miser* Dall, identified by Emery P. Chace of the San Diego Museum of Natural History. There were very few worm tubes or other obvious animals in the bottom sediment. It is possible that the constant sifting of the substrate by *P. planipes* in their search for food (Nicol, 1932) would reduce the numbers of any invertebrate animals having no defense against the crabs.

No crabs larger than 26 mm in standard carapace length (as measured from the notch between the rostral and subrostral spine and the median posterior margin of the carapace) have been found in plankton collections, and it has been assumed that this was their maximum size. However, at station 7 (depth about 300 m, see Fig. 2) the otter trawl and the closing dredge brought up crabs with a mean standard carapace length of 27.9 mm, and a maximum standard carapace length of 32.0 mm.

Juxtaposition of this size on a calculated growth curve (Boyd, 1967) suggests that these larger crabs living along the edge of the continental shelf constitute an older year class; they have probably completed their second year of life. Since no individuals of this size have been taken in the plankton, they are presumably exclusively benthic at this age. Station 7 was the deepest station from which crabs were dredged from the bottom. The mean length of the crabs caught from this deep station differed significantly ($p < 0.05$) from the mean lengths of crabs dredged from other stations, where the means did not differ from each other.

It appears that *P. planipes* lives to some extent on the bottom in its first two years of life and is also found as a planktonic animal at this stage. The relative amount of time spent in these two environments is unknown, but data from plankton collections indicate that there is some diurnal exchange between them, with crabs occurring in the surface water at night and settling to greater depths and perhaps to the bottom during the daytime hours (when a suitable bottom is available). After their sec-

ond year of life the crabs assume a strictly benthic existence and become segregated from younger animals by assuming a deeper environment.

The number of crabs per square meter of bottom may be roughly estimated by regarding the 10-ft otter trawl as a quantitative sampling device. At one station the trawl was towed for 25 minutes at two knots; it should have swept an area of 50,800 ft.^{2} The weight of the catch of crabs was estimated at 400–500 pounds. Since 100 crabs of the size caught in the trawl weighed 0.96 pounds, it is estimated that there were 0.8–1.0 crabs per ft^2 of bottom, or 9–11 crabs per m^2. Estimated densities for other stations were similar.

PELAGIC DISTRIBUTION

The center of the pelagic distribution (region of greatest abundance of crabs), as de-

lineated by data from the numerous plankton tows of the California Cooperative Oceanic Fisheries Investigations and miscellaneous cruises from Scripps Institution of Oceanography, is on the continental shelf of the western shore of southern Baja California. Presumably the crabs are distributed from this population center by the influences of the oceanic current systems. The surface circulation along the western coast of Baja California (Fig. 3) is complex, but in general there are two currents, acting in opposite directions (Reid, 1960). The more obvious of these is the California Current, which sweeps in a southerly direction along the California coast and swings westward in the latitude of southern Baja California. Its hydrography and fauna change gradually, and eventually it becomes or joins the North Pacific Equatorial Current. The effect of this southwesterly swing of the California Current on the distribution of *P. planipes* can
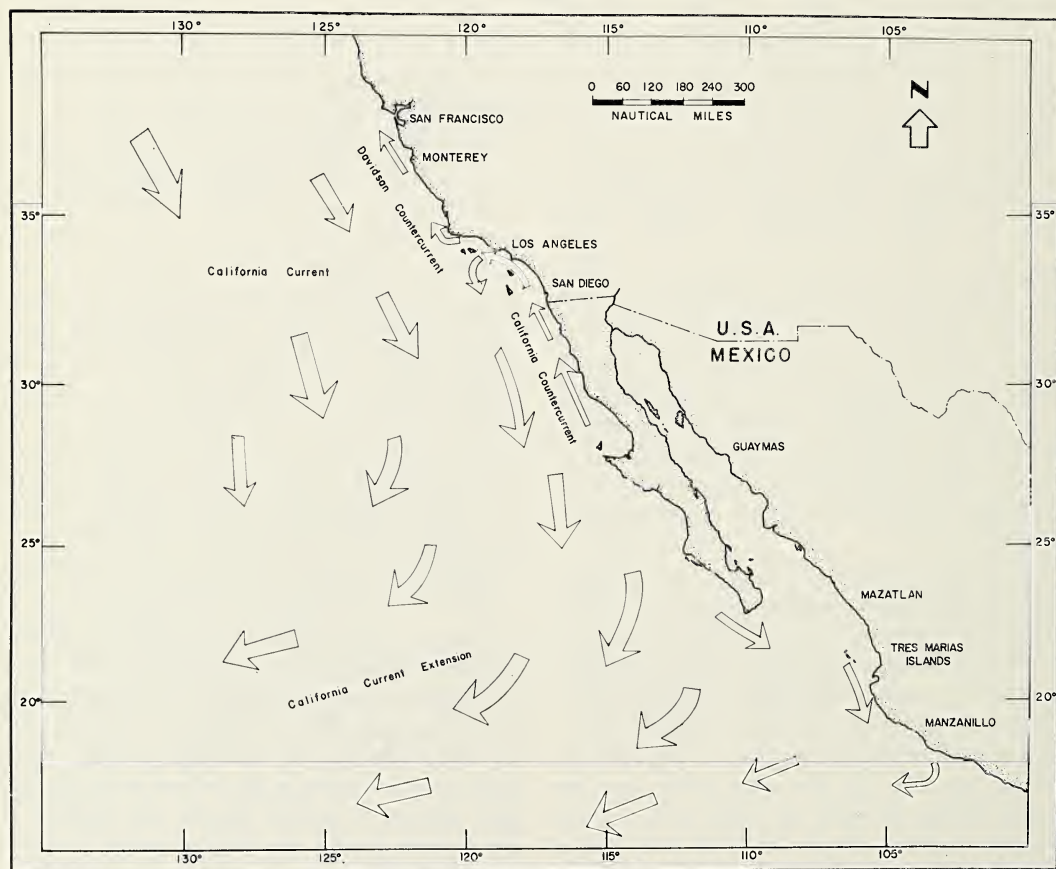
FIG. 3. A schematic presentation of the currents along the coast of California and Baja California.
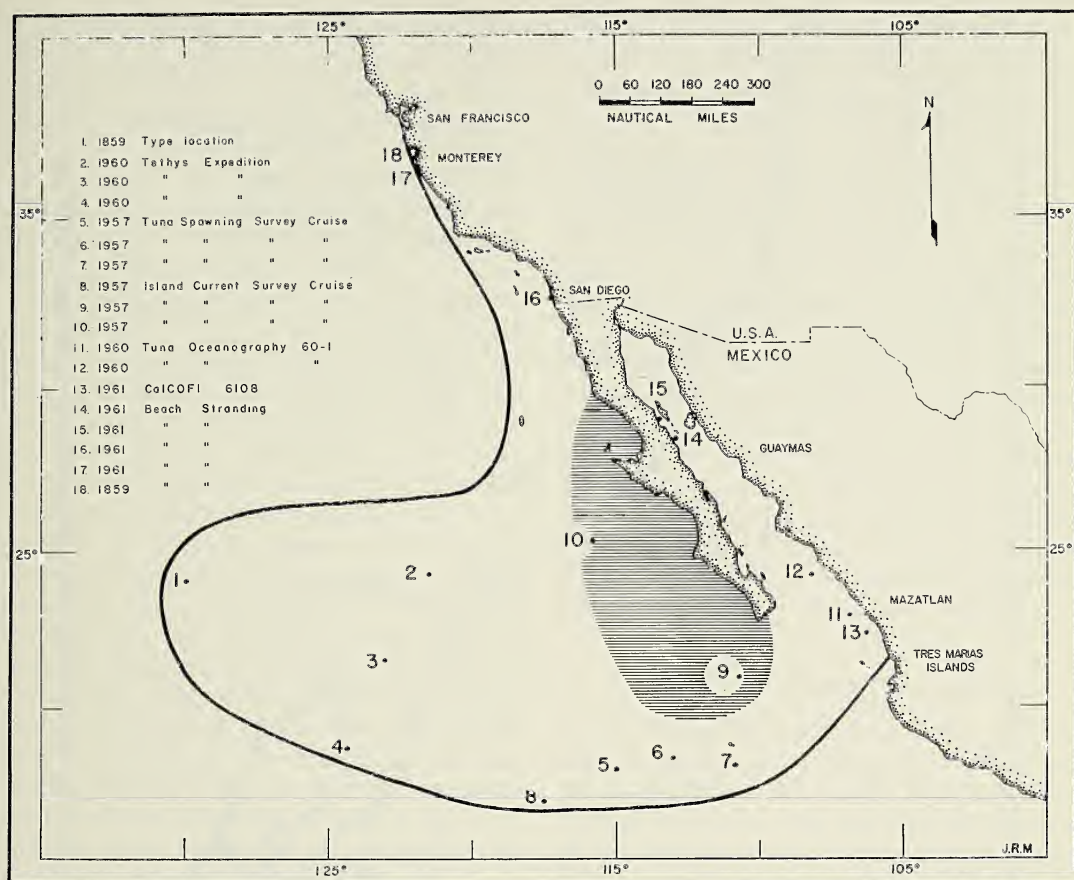
FIG. 4. Chart of outlying occurrences of *Pleuroncodes planipes* and the limits of distribution of the species. The *shaded area* indicates the region of greatest abundance.

be seen by examining Figure 4, which indicates the known range of the species. The western-most record is from the original species description by Stimpson (1860), at 24°N, 130°W, and is well within the North Pacific Equatorial Current. The few specimens that have been found in the western part of the range probably were swept away from coastal waters. These animals, caught in the Equatorial Current, may be assumed to be expatriates which do not contribute further to the maintenance of the species.

The occurrence of *P. planipes* north of its center of distribution depends upon a system of northerly-moving countercurrents. This system is composed of three parts which may have a common origin (Reid, 1960): (1) the Davidson Countercurrent, which flows northward very close to shore between Point Conception and the Oregon-Washington area; (2)

the Southern California Countercurrent, which moves nearshore water northward from southern Baja California and expands into a gyre inside the islands off southern California (Johnson, 1939), and then moves northward very close inshore around Point Conception; and (3) an undercurrent which transports deeper waters (at about 200 m depth) northward from Baja California. The undercurrent is the least understood of the three. The surface countercurrents are known to be seasonal, and have their strongest northward flow in January and February. These countercurrents account for the strandings of *P. planipes* at Monterey, California in March 1959 and again in January 1960.

The distribution of *P. planipes* in February 1960 (Fig. 5) is drawn from analysis of plankton samples taken by the California Cooperative Oceanic Fisheries Investigation's cruise
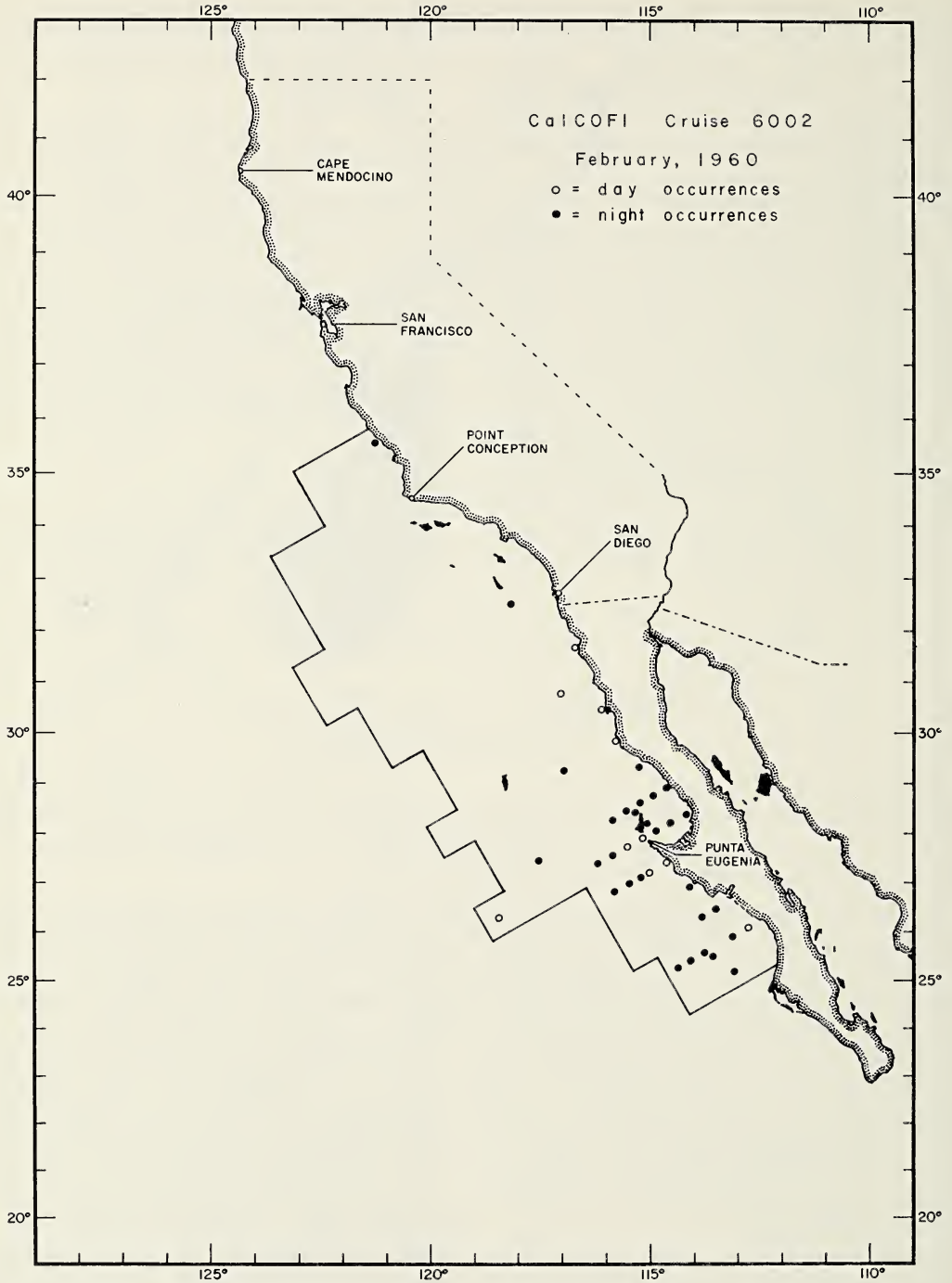
Fig. 5. Occurrences of *Pleuroncodes planipes* on CCOFI cruise 6002, February 1960. Oblique plankton tows from 140 m to the surface were taken with a meter net at stations about 40 miles apart on a grid plan. The area sampled is enclosed by the black line. Daytime captures are shown with an *open circle,* night-time captures with a *closed circle.*

6002. The specimens captured just south of Monterey represent the most northern intrusion of the animals during the period 1955–1960, and their occurrence in the plankton coincides with their stranding on the beach of Monterey in January 1960 (Glynn, 1961). The period between 1957 and 1960 was noted for the intensification of the countercurrent system and the intrusion of many southern forms into northern waters (Radovich, 1961).

The pelagic distribution of *P. planipes* in the Gulf of California is less well documented because only occasional cruises have been made there. The available data indicate that the crabs sometimes occur in abundance; for instance, large shoals of crabs were sighted in the northern half of the Gulf during the Vermillion Sea Expedition of the Scripps Institution of Oceanography in 1959. The crabs may have been swept in from areas on the western side of the peninsula as a consequence of the sporadic exchange of water between the California Current and the Gulf of California (see charts by Cromwell and Bennett, 1959). The alternative explanation is that the crabs were from a permanent population, even though the benthic habitat probably is very limited; the continental shelf is almost completely lacking in the Gulf, and the shore line drops off precipitously to depths of many hundreds of fathoms.

P. planipes has been captured more frequently during night hours than during daylight hours in the plankton tows of the CCOFI Cruises. In the monthly cruises 6001 to 6008 (January to August 1960), a total of 1,237 plankton tows were made within the region where *P. planipes* might be expected to occur; 601 were made at night and 636 in the day; 197 nighttime stations and 94 daytime stations yielded crabs. When these data are analyzed by 2×2 contingency analysis, the probability ($p < 0.01$) indicates higher nighttime capture. This analysis compared only positive and negative plankton tows and neglected the numbers of individuals caught. This information substantiates the picture of greater nighttime capture; during the March cruise (6003), 536 crabs were caught at night and only 96 in the daytime (the number of stations occupied at night was 71, and by day, 64). A chi-square test of the numbers of crabs caught at the

hourly intervals contrasted with the numbers expected at these hours if the crabs had occurred with the same frequency at all times indicates a highly significant difference in frequency ($p < 0.001$). This difference is due to the vertical migration of the crabs to the surface waters at night. The possible explanation that the crabs are avoiding the net during the day is rejected from analysis of a multiple linear regression (Boyd, 1967), indicating that larger crabs were caught during daylight hours; if the day-night abundance differences were due solely to avoidance, the larger animals presumably would have been able to avoid the net more easily than the small animals. While there is a tendency toward upward nocturnal migration it is by no means inviolate; crabs have often been sighted at the surface during the day. It is believed that in neritic waters the animals may settle to the bottom during the day when a suitable substrate is available.

SWARMS AND BEACH STRANDINGS

At times great numbers of red crabs are seen swimming at the surface of the ocean, particularly in the area along the western coast of Baja California. The late Bell M. Shimada of the Inter-American Tropical Tuna Commission reported (personal communication) steaming through such numbers that the "ship seemed to crunch through them for at least ten miles." Concentrations in excess of 100 crabs/m^2 of water surface over broad areas have been seen and photographed, but concentrations of 1–10 m^2 are more common. Reports by many individuals indicate that surface swarms may be sighted throughout the year, both night and day; the occurrence of the swarms does not seem to be associated with seasonal (winter) breeding cycles.

Mass mortalities of the crabs result when the swarms are washed up on the beach; it was such a stranding at Monterey, California in the winter of 1858 that resulted in the description of the species by Stimpson (1860). Many strandings were noted in 1958 and 1959 in the San Diego area, where the crabs had not been sighted in many years, and strandings on the beaches south of Punta San Eugenio are common.

All the crabs involved in the strandings that author has observed have been in the upper 50 cm of water in the surf zone. According to Inman and Quinn (1952) there is a net transport of this surface layer of water onto a beach with breaking waves. This onshore transport is balanced by water moving offshore in fast-moving rip currents and also along the bottom. The beach, then, is the ultimate destination of any object floating in the near-shore surface waters. An onshore wind and a receding tide hasten and intensify the stranding. The number of crabs involved in the strandings may be very large; one report (by George E. Lindsay, Museum of Natural History at San Diego, California, personal communication) from the Gulf of California notes the crabs occurring in windrows up to 3 ft deep and 10 ft wide over a stretch of beach 3–4 miles long.

PREDATORS

Presumably, when the crabs are in the pelagic phase they are preyed upon by large oceanic game fishes, notably albacore, yellowfin tuna, and skipjack tuna; these animals are not known to be bottom feeders. Alverson (1963) indicated that *P. planipes* constituted 78.1% of the volume of the yellowfin tuna's stomach contents in the area along the western coast of Baja California (approximately the area shaded in Figure 4). Around Alijos Rocks (24°57′N, 115°45′W) the percentage was as high as 97.5. *P. planipes* amounted to 34.1% of the volume of the stomach contents of all the yellowfin tuna caught and sampled in the entire eastern Pacific Ocean, and occurred in 39% of the stomachs which Alverson examined. He noted that *P. planipes* was also a significant food item for skipjack tuna as well as yellowfin tuna. McHugh (1952) found *P. planipes* comprised about 11% of the total volume of the contents of the albacore stomachs examined in his study; the percentage was higher (13–43) for those albacore which had been caught in areas where crabs were more abundant.

J. C. Quast (personal communication), in a survey of food habits of common kelp-bed game fishes along southern California, noted that these fishes were feeding on *P. planipes*

during the time of his study (1959). Among those fishes were kelp bass (*Paralabrax clathratus*), sheeps-head (*Pimelometapon pulchrum*), various rockfishes (*Sebastodes* spp.), senorita (*Oxyjulis californica*), and sculpin (*Scorpaena guttata*). Yellowtail (*Seriola dorsalis*) and white sea bass (*Cynoscion nobilis*) have been found to feed on *P. planipes* at the Coronado Islands, Baja California, Mexico. Bottom-living fishes are also known to feed on *P. planipes*; boccacio (*Sebastodes paucispinis*), the barber-pole fish (*S. rubrivinctus*), lingcod (*Ophiodon elongatus*), and various other species which had been feeding on *P. planipes* have been caught off La Jolla, California, at a depth of 330 ft.

SUMMARY

Pleuroncodes planipes has been found to exist as a benthic animal on the continental shelf of western Baja California, south of Punta San Eugenio. Two distinct populations seem to exist: a group of larger animals in their third year of life, or older, lives on the outer margin of the shelf; inshore of that group lives a population of animals in their first and second years of life. The smaller animals occupy the greater area, and exist in densities of 9–11/m² of bottom. Plankton tows made in this area and elsewhere indicate that the smaller crabs occur pelagically with a marked daily rhythm, being more abundant in the surface waters at night. When the crabs are in the plankton they are dispersed to the north by the coastal countercurrents and to the southwest by the California Current and Equatorial Current. When the crabs are at the surface they are fed upon by the tuna and albacore, and as the shoals of crabs are set on shore by wind and currents they are eaten by near-shore fishes or they may be stranded and die on the beaches.

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Some Inorganic Constituents of the Muscles and Blood of the Oceanic Skipjack, *Katsuwonus pelamis*[1]

Bryant T. Sather[2] and Terence A. Rogers

Cellular metabolism, anabolic and catabolic, regulates the production of macromolecules and the content of intracellular and extracellular ions. It is mainly the latter which are concerned with providing osmotic homeostasis. Much literature exists pertaining to the ionic composition of various tissues of aquatic and marine fish (Vinogradov, 1953). However, as noted by Love (1957), many of the values should be re-examined because of heterogeneity in sampling which makes comparisons almost impossible. Also, very little is known about the inorganic composition of a true pelagic form.

Only recently has it been possible to impound successfully for a fairly long period a fast swimming fish such as the oceanic skipjack, thus greatly enhancing the sampling of fresh tissues. Many of the fast-swimming pelagic fish have two distinct striated muscle types, white and red ("chiai"). When the tuna is cross-sectioned just anterior to the secondary dorsal fin, the two muscle types are readily discernible. The less plentiful red muscle pairs are located as bundles adjacent to the vertebrae. Both the dorsal and ventral pairs have horns that course, mediolaterally, toward the lateral line. At the skin the terminations of these horns are quite narrow. The remainder of the musculature is composed of the white muscle which approximately surrounds the red muscle bundles except at the lateral line.

Until recently, little was known about the physiological function of these two muscle types. It was thought that some indication might be obtained by determining the major electrolyte composition of the muscles and of the blood. Also, the inorganic components of the oceanic skipjack, *Katsuwonus pelamis,* may be very informative to the comparative physiologist as well as to the nutritionist.

MATERIALS AND METHODS

The tuna ("aku") were caught from a ship by the barbless hook-pole fishing method in waters adjacent to Oahu, Hawaii. The fish were transported to Oahu in large circular tanks with a constant supply of circulating sea water. The tuna were impounded in tanks similar to, but larger than, those aboard ship. The fish were fed frozen smelt and beef liver once a day, and were sacrificed for sampling 24 hours after feeding.

Cardiac blood was drawn into heparinized syringes. After the hematocrit was determined, the plasma was prepared. The pH of the plasma was determined by using the Beckman Model G pH-meter fitted with microelectrodes. The plasma's osmolality was ascertained employing the Fiske Osmometer.

The carcasses were sectioned, after which pieces (1.5–2.0 gm) of the two muscle types were removed. After weighing, one-half of the samples were dried overnight at 110°C and the percentage water content was determined. These samples were digested in concentrated nitric acid, appropriately diluted, and the sodium and potassium contents determined. The remaining samples were homogenized in 10% trichloroacetic acid (TCA), centrifuged, and the supernatants were drawn off for the calcium, magnesium, and chloride analyses.

The sodium and potassium content of the plasma and the muscles were determined by flame spectrophotometry employing a Coleman Jr. spectrophotometer equipped with a propane-oxygen burner. The plasma calcium was ascertained by the Ferro-Ham method (Ferro and Ham, 1957a and 1957b), using a Beckman

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Model B spectrophotometer. The Geyer and Bowie (1961) method was employed to determine the calcium content of the muscles. Both the plasma and muscle magnesium were estimated by the flame spectrophotometric method of Van Fossan et al. (1959). An organic diluting solution was substituted for acetone. The composition of the former was 500 ml isopropanol, 74.6 mg KCl, 292 mg NaCl, and 300 ml deionized water. The muscle calcium and magnesium and the plasma magnesium samples were determined on a Beckman Model DU spectrophotometer equipped with a hydrogen-oxygen burner and a photomultiplier. The muscle and plasma chloride contents were determined using a Buchler-Cotlove chloridometer.

To ascertain whether there was a difference in the electrolyte composition of the red and white muscles, the data were statistically analyzed employing the standard t-test for group comparisons.

To compare the muscle results with those of other investigators, the inulin space of the two muscle types was determined using C^{14}-inulin. The tissues (about 50 mg) were incubated in vitro at 20°C in tuna physiological saline containing 2900 cpm/ml of inulin. The composition of the saline was 19.99 mEq NaCl/liter, 7.52 mEq KCl/liter, 3.54 mEq $CaCl_2$/liter, 2.70 mEq $MgSO_4$/liter, 20 ml of phosphate buffer (pH = 7.4), and 4% glucose. At $\frac{1}{2}$, 1, 2, and 3 hours triplicate samples were removed from the media. After digestion in warm 30% KOH, 0.5-ml aliquots were transferred to pyrex planchettes and radioassayed on a Nuclear-Chicago Model 181 Scaler fitted with a DS-3 gas flow detector. All samples were corrected for self-absorption.

RESULTS

The data for the whole blood and plasma are contained in Table 1. The concentrations of the electrolytes and the osmolality are expressed in mEq/liter and mOs/liter, respectively. The bottom values under each column are the means ± the standard error of the means (S.E.).

The mean values for the blood components were as follows: hematocrit = 52.61%, pH = 7.32, osmolality = 414.56, sodium = 203.74, potassium = 6.81, chloride = 177.43, calcium = 7.56, and magnesium = 2.22.

The electrolyte data for the red and white

TABLE 1

BLOOD COMPOSITION OF *K. pelamis*

TUNA	HEMAT.	pH	OSM.[1]	Na[2]	K[2]	Cl[2]	Ca[2]	Mg[2]
1	56.0	7.50	450	200.3	4.70	178.00	7.81	3.35
2	54.0	7.18	416	196.2	6.78	189.67	7.92	2.27
3	45.0	7.38	400	194.9	5.71	186.67	6.54	1.66
4	48.0	7.30	396	185.5	6.56	176.00	7.14	1.30
5	51.0	7.29	394	186.2	9.64	171.00	7.46	1.80
6*	58.0	7.25	428	—	—	162.00	10.55	2.68
7*	52.0	7.38	445	231.8	2.81	189.00	7.08	4.05
8	48.0	7.41	400	200.0	7.50	176.00	7.04	1.55
9	39.0	7.33	401	200.5	5.97	176.00	6.28	1.53
10*	59.0	7.41	436	222.7	3.85	182.00	9.41	3.18
11*	59.0	7.42	425	213.6	8.85	181.00	7.64	2.32
12*	55.0	7.22	426	211.4	8.71	177.00	8.37	2.70
13	52.0	7.31	406	200.0	11.60	176.50	6.51	1.45
14	53.0	7.22	416	202.5	8.10	175.00	7.43	2.35
15	51.0	7.18	414	209.5	3.80	174.50	7.46	1.72
16	46.0	—	397	201.0	7.60	173.00	6.19	1.59
17*	57.0	—	398	—	—	173.00	7.22	2.00
18	64.0	—	414	—	—	—	8.13	2.41
Mean	52.61	7.32	414.56	203.74	6.81	177.43	7.56	2.22
S.E.	1.417	0.025	4.082	3.216	0.624	1.652	0.256	0.177

* Hemolyzed blood.
1 Osmolality values in mOs/liter.
2 Electrolyte values in mEq/liter.

TABLE 2

Red Muscle Composition of *K. pelamis*[1]

TUNA	% H_2O	Na	K	Cl	Ca	Mg
1	70.99	26.50	75.70	—	—	11.80
2	—	22.12	75.32	0.0	0.00	18.43
3	—	26.94	74.56	0.0	0.86	20.26
4	72.83	29.14	80.40	—	0.51	8.49
5	75.64	22.62	73.35	—	9.11	11.72
6	72.49	21.32	92.65	—	3.04	21.98
7	72.60	15.80	91.80	15.96	0.66	21.59
8	72.03	18.36	76.26	—	1.56	19.44
9	75.09	26.53	78.66	52.17	1.07	18.24
10	72.90	20.30	94.40	42.14	—	—
11	72.31	18.74	94.40	61.74	0.93	21.29
12	72.08	25.18	78.06	—	1.40	18.43
13	73.53	14.56	69.86	—	1.45	19.06
14	72.16	16.93	75.83	38.74	1.22	16.95
15	72.18	14.63	71.80	28.10	1.78	17.09
16	73.46	20.30	80.40	67.03	4.70	14.70
17	73.42	18.40	84.40	55.58	0.78	14.51
18	70.79	18.10	80.10	73.66	0.74	16.02
Mean	72.78	20.92	80.44	39.56	1.86	17.06
S.E.	0.318	1.050	1.853	7.48	0.557	0.920

[1] Electrolyte values in mEq/kg fresh wt.

TABLE 3

White Muscle Composition of *K. pelamis*[1]

TUNA	% H_2O	Na	K	Cl	Ca	Mg
1	71.75	16.20	94.60	—	58.80	19.70
2	—	9.12	98.79	23.58	7.12	27.29
3	—	17.16	109.38	—	5.00	26.38
4	76.91	17.44	113.52	—	0.94	17.13
5	80.24	22.41	113.44	—	0.44	16.49
6	72.13	7.26	88.35	0.00	3.99	33.79
7	71.34	9.23	113.35	0.00	0.52	31.71
8	73.97	9.20	116.70	0.00	1.48	25.49
9	76.69	26.71	109.36	77.34	2.34	24.38
10	71.25	6.95	94.20	87.57	0.00	35.02
11	76.65	9.89	114.60	91.36	0.00	23.98
12	73.19	3.61	125.90	44.73	0.83	27.59
13	75.14	7.14	95.53	36.93	1.25	25.86
14	74.16	8.12	108.43	55.56	1.85	25.20
15	74.42	7.18	100.73	52.80	0.93	22.78
16	75.44	11.50	108.50	20.30	2.86	20.42
17	75.28	8.70	105.00	16.23	0.18	18.95
18	73.29	9.70	104.40	19.92	0.27	21.90
Mean	74.49	11.53	106.38	37.59	4.93	24.67
S.E.	0.603	1.422	2.255	8.480	3.200	1.241

[1] Electrolyte values in mEq/kg fresh wt.

muscles comprise Tables 2 and 3, respectively. As in the former table, the last values are the means ± the S.E. The values in these tables, excluding the water content, are in mEq/kg fresh weight. A brief resume of the statistical comparisons is contained in Table 4.

The inorganic contents of the red and white muscles, respectively, were: water = 72.78,

TABLE 4

VALUES OF T-TESTS FROM DATA IN TABLES 2 AND 3.

ELECT.	MUSCLE	MEAN (mEq/kg)	MEAN$_1$-MEAN$_2$	CALCULATED t-VALUE	P VALUE
% H$_2$O	red	72.78			
	white	74.49	2.0	2.947*	0.01
Na$^+$	red	20.92			
	white	11.53	9.39	5.314*	0.001
K$^+$	red	80.44			
	white	106.38	25.94	8.890*	0.001
Ca^{++}	red	1.86			
	white	4.93	3.07	0.892	0.40
Mg^{++}	red	17.06			
	white	24.67	7.61	4.744*	0.001
Cl$^-$	red	92.16			
	white	68.76	23.40	0.549	0.50

* Significant difference.

74.49%; sodium = 20.92, 11.53; potassium = 80.44, 106.38; calcium = 1.86, 4.93; magnesium = 17.06, 24.67; and chloride = 92.16, 68.76.

Statistical differences between the means demonstrated that only the calcium and chloride contents of the two muscle types were not significantly different.

The uptake of the C^{14}-inulin by the two muscle types is illustrated in Figure 1. The two intercepts at the ordinate were fitted by eye. The values for the red and white muscles are 0.69 and 0.55 cpm/mg fresh weight, respectively. The calculated extracellular (inulin) space for the red muscle is 23.79% and that of the white muscle is 18.97%.

Table 5 contains the comparison of some plasma constituents of various fishes with those of the skipjack, K. pelamis. The plasma concentrations are in mEq/liter.

The comparison of the muscle electrolyte contents of some teleosts with those found in the skipjack is contained in Table 6. The concentrations are expressed in mEq/kg tissue water.

DISCUSSION AND CONCLUSIONS

The blood constituents of K. pelamis (Table 1) will be discussed with comparable data from other species in a later section of this presentation.
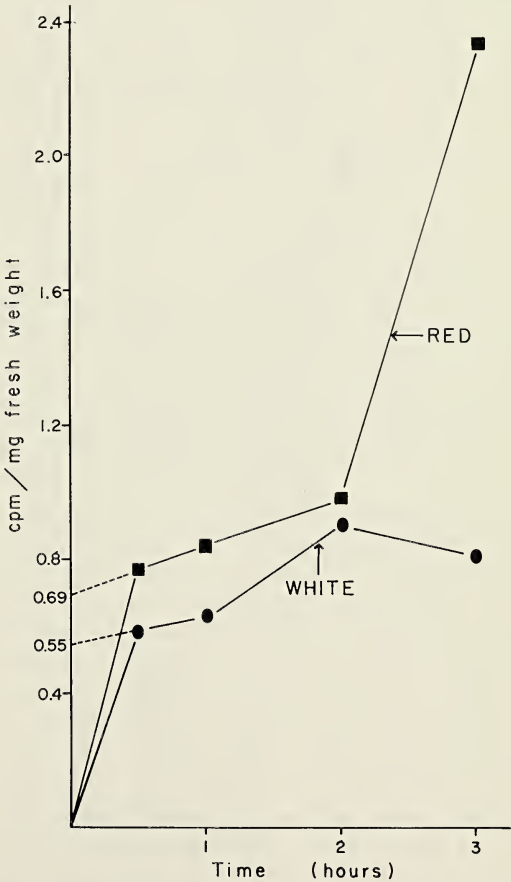
FIG. 1. Uptake, in vitro, of C^{14}-inulin by red and white muscles of the skipjack, K. pelamis.

TABLE 5

COMPARISON OF SOME PLASMA CONSTITUENTS OF VARIOUS MARINE FISHES

FISH	Na[1]	K[1]	Cl[1]	Ca[1]	Mg[1]	OSM.[2]	REFERENCE
Cyclostomata							
Polistotrema stoutii (hagfish)	544	7.7	446	10.8	20.8		Urist (1963)
Myxine glutinosa (hagfish)	558	9.6	576	12.4	38.8		Robertson (1960)
Chondrichthyes							
Raja erinacea (skate)	254	8	225	12	5	1035*	Hartman et al. (1941)
Narcine sp.	134	7	159	24	6		Salome Pereira and Sawaya (1957)
Rhinobatus sp.	143	12.8	143.6	14.6	4		Salome Pereira and Sawaya (1957)
Triakus semifasciaus (shark)	235	10	230	10	6		Urist (1962)
Teleostei							
Muraena ? atlanticus (eel)	101	6.2	140	5.0	2.4		Urist (1963)
Muraena belena (eel)	212	1.95	188	7.74	4.84		Robertson (1960)
Lophius piscatorius (goosefish)	193	5	153	12	10	431*	Brull and Cuypers (1955)
Lophius piscatorius (goosefish)	185	5.1	153	6.4	5.0		Robertson (1954)
Paralabrax clatbratus (kelp bass)	180	5.0	147	6.0	3.0		Urist (1962)
Scomberomorus maculatus (mackerel)	198	10.3	176				Becker et al. (1958)
Clupea barengus (herring)						512	Holliday and Blaxter (1961)
(barracuda)	215	6.4	189				Becker et al. (1958)
Mycteroperca bonaci (grouper)	237	8.2	217				Becker et al. (1958)
Katsuwonus pelamis (skipjack)	204	6.8	177	7.6	2.2	415	authors (1966)

[1] Electrolyte values in mEq/liter.
[2] Osmolality values in mOs/liter.
* From Potts and Parry (1964).

The data contained in Tables 2 and 3 were analyzed statistically to determine whether the concentrations differed with muscle type; these results are presented in Table 4. The white muscle contains a greater amount of water, potassium, and magnesium which possibly indicates that this tissue has a larger intracellular space. Statistical differences in the calcium and chloride contents were not found, which may have been due to the TCA used in the extraction. However, blanks were carried throughout the analysis.

Figure 1 illustrates that the extracellular volume of the red muscles is greater than that of the white. The calculated inulin spaces for the red and white muscles are 23.79 and 18.97%, respectively. The higher sodium content of the red muscle verifies the larger extracellular space.

It was not possible to determine accurately the intracellular sodium and chloride contents because of their high content in the intravascular compartment. The other intracellular calculated concentrations (mEq/liter cell water) of the red and white muscles, respectively, were: potassium = 160.88, 189.28; magnesium = 33.76, 43.68; calcium = 0.12, 6.30.

It is well known that the amount of intracellular potassium determines the threshold value for any tissue. Thus, the potential produced by this ion for the red muscle was calculated to be 83.77 mv and that of the white muscle was 88.08 mv—a potential difference of 4.31 mv. Therefore, the red muscle would have a lower threshold value, indicating that possibly this muscle would be utilized more than the white.

Vernick (1964) reported that the red muscle of four pelagic species had a higher content of thiamine, riboflavin, pantothenic acid, vitamin B_{12}, myoglobin, and cytochrome C. This tissue also had a higher degree of vascularization and larger mitochondria in the sarcoplasm. These findings led to the suggestion that the red muscle provided energy for the white. Hamamoto and Hohl (personal communication) discovered that the mitochondrial density in the red muscle sarcoplasm of *K. pelamis* was approximately one magnitude greater than that in the white. Because the mitochondria are the cell's energy producers, there is a strong correlation between the degree of activity of the muscle and the number and shape of the mitochondria within the muscle cells (Davson, 1964). In addition, if one considers the color of the two muscle types and applies the analogy of the breast muscles of chickens versus those of the pigeon, it becomes apparent that the red muscle of *K. pelamis* with its abundance of mitochondria is possibly used for swimming and not as an energy producer for the white muscle. The red muscle is, indeed, able to contract and is probably used for normal swimming activity (Rayner, personal communication). The white muscle may be used secondarily, e.g., for accelerated and rapid movements seen during avoidance and feeding reactions.

Table 5 lists some of the plasma constituents of various fishes. It is well known that the marine cyclostomes are approximately isosmotic to the medium and that the marine cartilaginous fishes are hyperosmotic to the environment. However, the sea water-inhabiting teleosts are hyposmotic to their medium. Thus, these animals are threatened by desiccation. To prevent dehydration the animals must drink water and selectively excrete ions. The latter process is generally accomplished extrarenally via the gills.

Of the teleosts listed in Tables 5 and 6 only the barracuda and herring can be comparable to the skipjack, and the eels would be intermediate in comparison; the other species would be least comparable due to their phylogenetic placement and their relative inactivity as compared with the scombroid fishes. The mackerel is a scombroid fish, but it inhabits more inshore waters than does the skipjack.

As expected, the electrolyte composition of the skipjack plasma (Table 5) is less than that of the cyclostomes. However, it approximates those of the chondrichthyes. The greater osmolality of the latter is due to a higher urea content of the plasma. Concentrations of 300–400 mM of urea and trimethylamine oxide/liter are essential for elasmobranch osmoregulation (Urist, 1962). The plasma calcium and magnesium in the skipjack are much less than those in the chondrichthyes. This can be attributed to the apatite, which allows the teleost to maintain ionic concentrations independent of the external medium, and to the greater efficiency of the kidney and possibly the gills.

TABLE 6

COMPARISON OF SOME MUSCLE CONSTITUENTS OF SOME MARINE TELEOSTS[1]

FISH	Na	K	Cl	Ca	Mg	REFERENCE
Muraena helena (eel)	25.0	165	23.7	18.7	14.9	Robertson (1960)
Mycteroperca bonaci (grouper)	51.5	125.5	26.7			Becker et al. (1958)
Scomberomorus maculatus (mackerel)	71.7	153.5	53.8			Becker et al. (1958)
Clupea pilchardus (herring)	53.8	170.6	65.6	152.1	51.3	Carteni and Aloj (1934)
Katsuwonus pelamis (skipjack)						
Red muscle	35.46	136.36	67.06	3.15	28.92	authors (1967)
White muscle	20.77	191.61	67.71	8.88	44.43	

1 Values in mEq/kg water.

The plasma sodium content of the skipjack is greater than those of the Atlantic eel, the goosefish, and the kelp bass, but is lower than those of the Roman eel, the barracuda, and the grouper. The same order is found for the skipjack when the chloride values are compared. In comparing the potassium values, the Atlantic eel and the barracuda have similar concentrations of plasma chlorides. The Roman eel, the goosefish, and the kelp bass have lower plasma chlorides than the skipjack. In *K. pelamis,* lesser concentrations of plasma sodium, potassium, and chloride are probably due to differences in the osmoregulatory mechanism and the type of integument. Excluding the mackerel and possibly the barracuda, the listed teleosts are not true pelagic species and may be subjected to some degree of salinity fluctuations. In Hawaii, the barracuda is frequently seen in shallow lagoons which are subjected to dilutions during heavy rains.

Comparison of the plasma calcium of the listed teleosts shows that only the goosefish (Brull and Cuypers, 1955) had a higher plasma content. The value reported by Robertson (1954) appears to be in agreement with those reported by the other investigators. It is also apparent that the plasma magnesium of *Lophius* is greater than those reported by the other authors. It is known that temperature plays an important role in the solubility product constant of compounds and, thus, the rate of ionic exchange in apatite. A higher body temperature coupled with high serum alkaline phosphatase activity and other factors would favor a decrease in blood calcium, phosphate, and magnesium. It has been reported that tunas and skipjacks have body temperatures 6°–12°C

higher than their environment (Kishinouye, 1923; Berg, 1940; Morrow and Mauro, 1950; and Van Oosten, 1957). It would be expected, then, that the blood calcium and magnesium content of the skipjack would be less than that found in the colder poikilothermic fishes, but greater than that found in mammals. This is apparent for the magnesium values but not for those of the plasma calcium. Also, there is a correlation between the activity of species and the amount of plasma magnesium. The more active forms generally have lesser concentrations of plasma magnesium. The greater blood calcium level of the skipjack, excluding the value of Brull and Cuypers, may be due to the intrinsic factors controlling osteogenesis and the amount of apatite coupled with the efficiency of the kidney, the ionic strength of the serum, and the amount of vitamins A and D stored in the liver.

In brief, the differences in blood ionic concentrations of various fishes is greatly influenced by the type and composition of the skeleton. Apatite not only stores Ca^{+2} and PO_4^{-2} but also Na^+, Mg^{+2}, and CO_3^{-2}. The regulation of K^+ and Cl^- is influenced not by the skeleton but by the gills and kidneys. Osmoregulation is delicately controlled by enzymes, hormones, and vitamins. The amounts and activities of these complexes are influenced by intrinsic and extrinsic factors which affect cell permeability and metabolism in such a way that each organism is unique in its electrolyte composition.

Comparative values of some muscle electrolytes of marine teleosts are presented in Table 6. The ionic composition of the plasma definitely influences that of the surrounding tissues.

Fish with high plasma electrolyte values usually have tissues with relatively high electrolyte values. The grouper, mackerel, and herring have greater amounts of muscle sodium than does the skipjack. The sodium content of the muscles of the eel is intermediate between the skipjack's red and white muscle content. This is to be expected because the plasma sodium of *K. pelamis* closely aproximates that of the eel. However, it is also apparent that the blood sodium of the mackerel and the skipjack are present in nearly equal concentrations. At first glance the difference in the muscle sodium content of the two species is obscure, but it will be recalled that the body temperature of tuna is 6°–12°C higher than their environment and, therefore, the muscles of the skipjack would probably be more active metabolically than those of the mackerel. If this is truly the case, the sodium pump of the skipjack would be much more efficient, thus producing a lesser intracellular sodium content than that present in the mackerel and possibly in the other higher teleosts.

Upon comparing the potassium content of the various muscles, it becomes apparent that the plasma content does not necessarily influence the muscle content. This is obvious on examining the values for *Muraena* and *Scomberomorus*. The plasma potassium content of the former animal is 1.95 mEq/liter in contrast to a muscle content of 165 mEq/kg water. The potassium content of the plasma for *Scomberomorus* is 10.3 mEq/liter as compared with a muscle content of 153 mEq/kg water. Also, on examination of the blood and muscle concentration of the teleosts, no obvious order is evident, e.g., the blood potassium order is: mackerel > grouper > skipjack > eel, and the muscle order is: skipjack white > eel > mackerel > skipjack red > grouper. It appears, therefore, that the difference in muscle potassium may be under greater metabolic control than is sodium. Thus, the extracellular potassium may be entirely under the influence of the hormonal and genetic composition of the animal.

The chloride content of a tissue, like the sodium content, is greater extracellularly than intracellularly. It would then be expected that the chloride content of the muscles would parallel that of the plasma. However, the data in

Tables 5 and 6 do not support this hypothesis. The importance of chloride in a tissue is to maintain electrochemical neutrality. Thus, the chloride content of a tissue is maintained passively as a result of the Na^+ and K^+ distribution. As noted above, this ionic distribution is genetically influenced and thus the Cl^- distribution would subsequently be controlled but in a more subtle manner. Further examination of Table 6 reveals that the muscle and blood chlorides of the grouper are greater than those of the eel, and also that the chloride values for the skipjack are greater than those of the mackerel. However, the relationship between blood and muscle chlorides terminates at this point, because the skipjack muscles have the greatest chloride content, but the plasma chloride content is intermediate between those of the eel and the mackerel.

It is not possible to make similar comparisons with the herring because the blood values of this fish could not be located. Such data would be informative because the herring is more closely related systematically and ecologically to the skipjack than to the eel and grouper.

The data for muscle calcium and magnesium of marine teleosts are very meager. In Table 6 only one direct comparison can be made, that between *M. helena* and *K. pelamis*. The values for the herring cannot be considered because, as was noted by Robertson (1960), the muscle samples were contaminated with bone fragments. The calcium content of both muscle types of the skipjack is less than that of the eel, although the blood calcium levels of both species are approximately the same.

The results of the comparison of the magnesium contents are opposite to those of the calcium comparison. The eel has about twice the amount of blood magnesium that the skipjack does. The differences in the muscle content are that the red muscle of *K. pelamis* has about twice the amount, and the white muscle has about three times the amount found in the eel. This may be due to a greater preponderance of myosin and adenosine triphosphate (ATP) in the muscles of the skipjack.

It is known that magnesium serves as a cofactor for bridging ATP and creatine to the creatine kinase molecule during transphosphorylation (White et al., 1964). It is quite pos-

sible that the muscle ATP content of fast swimming fish is greater than that in less active forms. Studies on the phosphorus compounds of fish muscle may produce a strong correlation between magnesium and ATP-creatine phosphate contents.

SUMMARY

1. The major electrolyte constituents of the plasma, red muscle, and white muscle of the oceanic skipjack, *Katsuwonus pelamis*, were determined. The potassium content and the greater mitochondrial density of the red muscle suggest that this muscle is utilized for normal swimming activity rather than being an energy source for the white muscle.

2. The plasma electrolytes were compared with those of other marine fishes. In general, the sodium content of the skipjack plasma is less than that found in the cyclostomes, the skate and the shark, but is slighly greater than that found in the majority of other teleosts. The plasma potassium is less than that in the cyclostomes and elasmobranchs and greater than that in other teleosts. The plasma chloride content of the skipjack, as well as the calcium and magnesium, is less than that of the other investigated species.

3. Comparison of the differences in the electrolyte composition of the red and white muscles reveals that the white tissue contains a larger amount of water, potassium, and magnesium. However, the red muscle contains a greater amount of sodium.

4. Using C^{14}-inulin, the extracellular space of the red and white muscles was determined to be approximately 0.24 l/kg muscle and 0.19 l/kg muscle, respectively.

5. The muscle electrolyte content of *K. pelamis* was contrasted with the muscle contents of other teleosts. The order of decreasing composition is as follows. For Na^+: mackerel > herring > grouper > skipjack red > eel > skipjack white; for K^+: skipjack white > herring > eel > mackerel > skipjack red > grouper; for Cl^-: skipjack red > skipjack white > herring > mackerel > grouper > eel. Both muscle types of the skipjack contained less calcium and more magnesium than did the muscle of the eel.

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The Systematics of the Prickly Sculpin, *Cottus asper* Richardson, a Polytypic Species

Part II. Studies on the Life History, with Especial Reference to Migration[1]

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ABSTRACT: The occurrence of a downstream spring migration of weakly-prickled *Cottus asper* in coastal streams is confirmed and documented. Successful intertidal spawning and incubation is followed by a pelagic larval stage of about one month. Metamorphosis occurs and the prejuveniles settle to the bottom to feed in the estuarine portion of the river. An upstream migration of adults precedes that of the young-of-the-year in late summer. During the non-migratory phase, prickly sculpins are located in the low gradient, low velocity portions of coastal streams.

Densely-prickled *Cottus asper* living in distant inland waters, where access to the sea is almost impossible, undertake only local migratory movements. Densely-prickled forms living in some inland lakes and streams relatively close to the sea, where access to the sea is open and relatively easy, do not migrate seaward but undertake only local movements to spawn in fresh water. The present study discusses differences in migratory behavior between "coastal" and "inland" prickly sculpins.

THE EXISTENCE of a seaward spawning migration of prickly sculpins in coastal streams has been suggested, or implied, for at least 30 years (Taft, 1934; Pritchard, 1936; Sumner, 1953; Shapovalov and Taft, 1954; Hunter, 1959; and McAllister and Lindsey, 1959). Although some of these authors have observed the presence of reproductively mature *Cottus asper* in the intertidal areas of coastal streams, none has demonstrated that intertidal spawning actually occurs.

Populations of *C. asper* occurring in lakes and streams far enough inland to preclude the possibility of an annual seaward spawning migration are presumed to spawn in fresh water. The approximate or exact spawning sites of some of these populations have now been determined from the presence of larvae (Nicola Lake, British Columbia), and egg clusters or gravid females (Pothole Lake, near Merritt, British

Columbia). Other localities are close enough to the sea to imply the existence of a short seaward migration on the part of the *C. asper* populations living therein, but access to the sea is prevented by natural or man-made barriers, e.g., at Buttle Lake and Horne Lake, on Vancouver Island, British Columbia. Spawning of prickly sculpins in these areas is necessarily restricted to fresh water.

Still other localities, frequented by migratory salmonids, are close enough to the sea to permit a seaward migration on the part of *C. asper* living there, but it does not occur. For example, these spawning sites of the following prickly sculpin populations in the lower Fraser Valley in British Columbia are known from capture of gravid fish and/or egg masses: South Alouette River; Kenworthy Creek and Chilqua Slough (both are inlet streams to Hatzic Lake); Squakum Lake (Lake Erroch); and Cultus Lake. In addition, spawning fish have been captured in inlet streams of Skidegate Lake, in the Queen Charlotte Islands, along with migratory juvenile salmonids. The outlet of Skidegate Lake is only about 13 miles from the sea. A newly hatched larva of *C. asper* (?) has been taken in a

plankton net in the Second Narrows region of Owikeno Lake (about 30 miles from the sea), on the coast of central British Columbia. It is presumed that the parents spawned in fresh water.

MATERIALS AND METHODS

To document the supposed occurrence and to determine the success of intertidal spawning of prickly sculpins in the coastal streams, the Little Campbell River (Fig. 1, site 2) was chosen as a study stream. In 1960–1961, a series of 18 permanent collecting sites (Fig. 2) was sampled at biweekly intervals for a period of one year, and at monthly intervals for an additional six months. The lower reaches of the river, stations C-1 to C-3, were also sampled several times in late winter and early spring of 1962 and 1963, to obtain live specimens for laboratory studies. Additional live specimens for use in laboratory studies were collected from the following localities (Fig. 1): site 1, Nile Creek and Big Qualicum River, Vancouver Island; site 3, South

Alouette River; site 4, Kenworthy and Edwards creeks (Hatzic Lake); site 5, Sweltzer Creek (outlet of Cultus Lake); and site 6, Squakum Lake (Lake Erroch).

A 3 mm-mesh, woven-nylon seine, 3 m wide $\times$ 2 m deep, was mounted on collapsible telescoping aluminum poles and used for all field collections. Salinities were measured with density hydrometers.

SAMPLING LOCALITIES AND STUDY STREAM

The primary study area was the Little Campbell River (Campbell Creek), which is approximately 15 miles long and empties into Semiahmoo Bay between White Rock, British Columbia and Blaine, Washington (site 2, and inset of Fig. 1). The stream's drainage area is approximately 28 square miles.

Collection sites are shown in Figure 2. Station 0-1 is located on a sand-mud flat outside the main river channel. Station C-0 is located below the railroad trestle at the mouth of the river in the main channel, station C-1 about 50
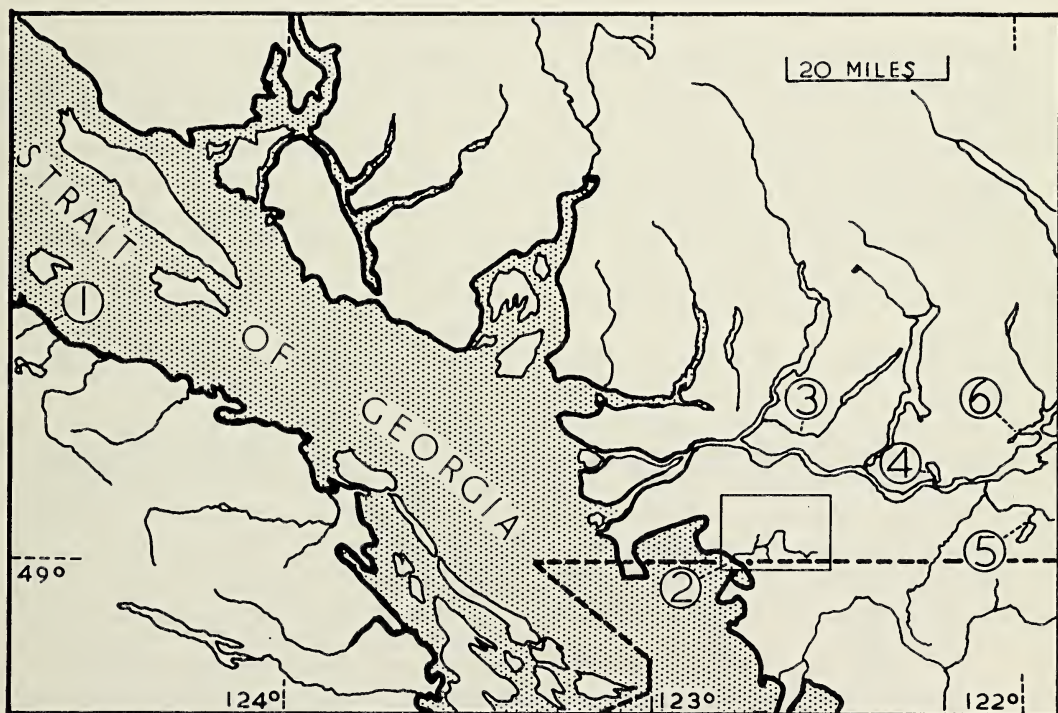
FIG. 1. Localities for spawning populations of *Cottus asper* used in life history studies. Site 2 (inset) is expanded in Figure 2. Other site localities are listed in text.
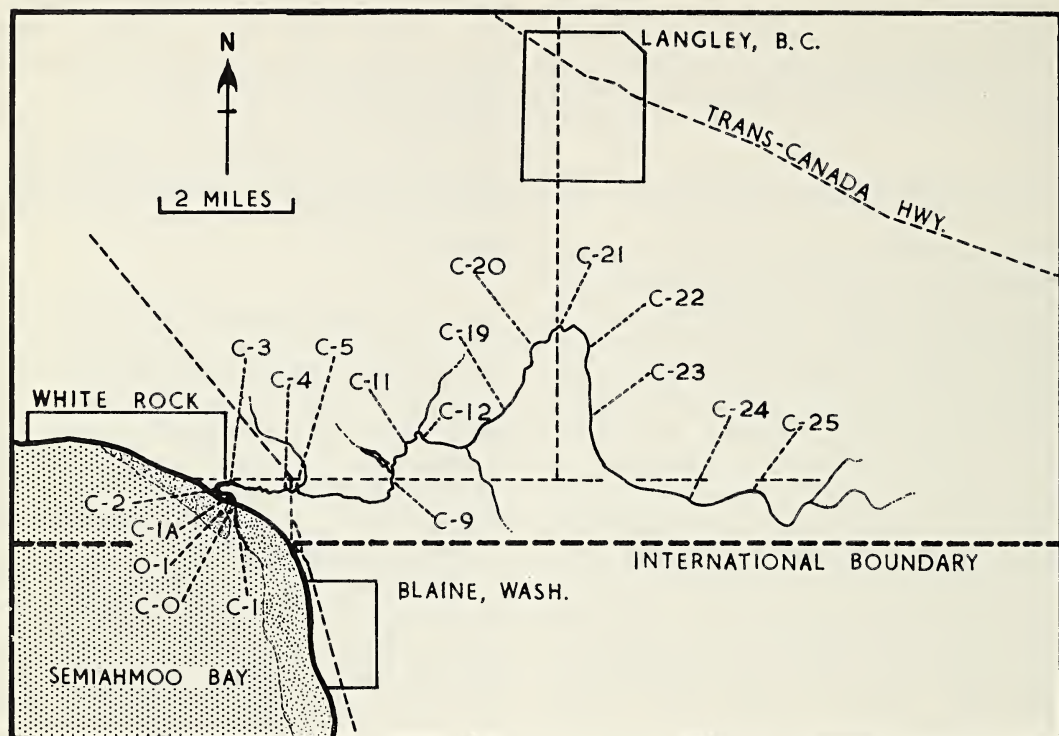
FIG. 2.   Collection sites within the Little Campbell River.

yards inside the mouth, and station C-1A about 75 yards inside the mouth. Station C-2 is located $\frac{1}{4}$ mile, and C-3 $\frac{1}{2}$ mile, from the mouth. Figure 3 shows the collection sites in relation to stream gradients, and maximum upstream effects of tidal fluctuations in salinity and depth. Stations C-0 through C-9 are all subject to tidal fluctuations in depth, whereas stations C-0 through C-3 are tidally inundated with mixohaline waters.

Barnacles (*Balanus* sp.) are found at stations C-0 through C-3, and permanent beds of the oyster *Crassostrea gigas* are located between stations C-1 and C-1A, and at C-2. Typical fish associates in areas C-0 through C-3 are *Leptocottus armatus, Platichthys stellatus,* and, throughout the summer, young-of-the-year *Cottus aleuticus. Oligocottus maculosus* and *Clinocottus acuticeps* are commonly found upstream as far as station C-2.

RESULTS OF FIELD STUDIES

The prickly sculpin is distributed primarily in the lower 4 miles of the Little Campbell River.

Especially in spring, 1961, an increased number of *C. asper* were present in the lower reaches of the river, around the spawning site (station C-2). Over the first 9-month sampling period, no *C. asper* were captured in stations upstream of C-22. With three exceptions, none was taken in the fast-flowing, high gradient area of the stream below C-20 and above C-11 (Fig. 3). This area is densely populated with the coast range sculpin, *Cottus aleuticus.* Figure 4 illustrates the disjunct distribution of yearlings, subadult, and adult prickly sculpins.

From late February to early March the prickly sculpin undertakes a migration downstream to the estuary. The only area in the lower 4 miles of stream in which suitable spawning substrate (large cobbles, flat rocks) occurs is a stretch about 100 yards long lying $\frac{1}{4}$ mile upstream from the mouth (station C-2, Figs. 2 and 3). The males, which come into spawning condition earlier in the season than the females (see below), select nesting sites under large cobbles or flat rocks in the stream bed in areas of current velocities equal to or less than 1 cubic ft/second (at low tide). Apparently it is im-
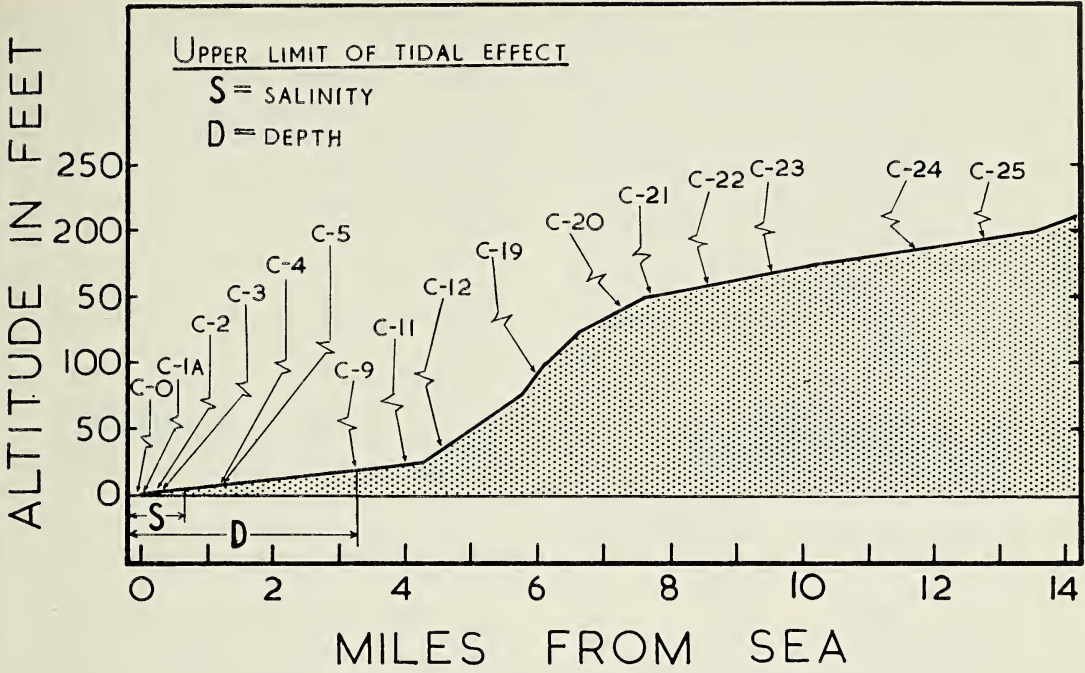
FIG. 3. Little Campbell River collection sites in relation to stream gradients and tidal influence. See text for explanation.
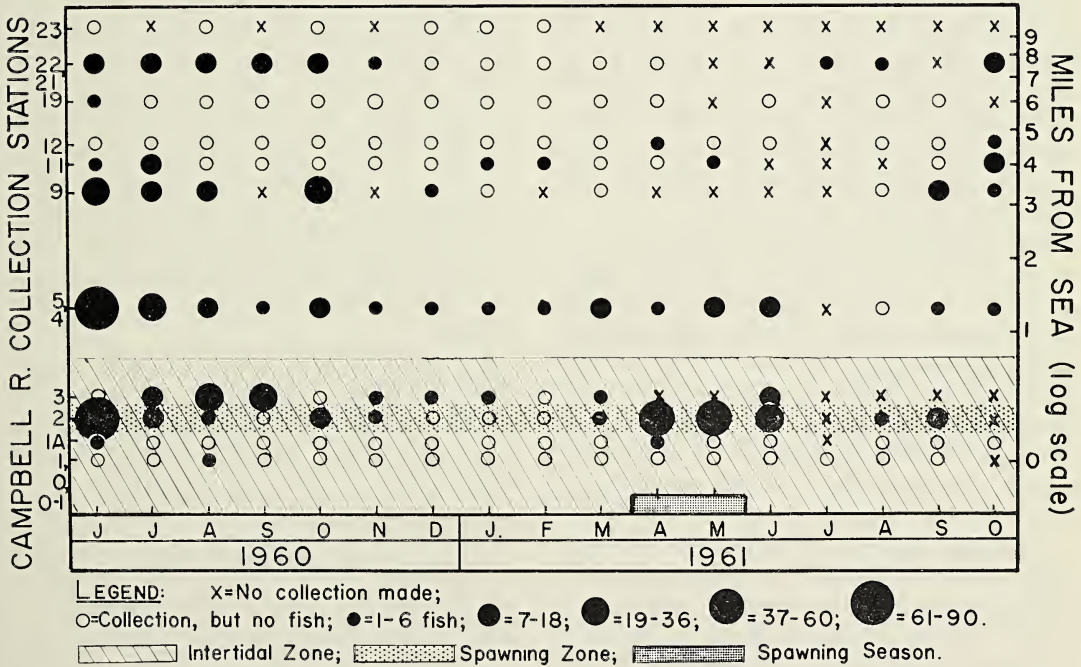
FIG. 4. Monthly distribution of yearling, subadult, and adult *Cottus asper* within the Little Campbell River. Data taken from pooled biweekly samples representing results of 700 seine hauls.

portant that the substrate surface be relatively rough in texture, since the adhesive eggs adhere only temporarily to a smooth surface such as glass or plastic. Old automobile exhaust pipes, or muffler tubes, are "preferred" nesting sites when available in the environment (as they are in the Little Campbell River).

Females aggregate upstream (about station C-3) above the main spawning area and then move individually onto the spawning beds where they display to, and are courted by, males both outside and inside their nests. After a male selects a female to occupy his nest, further courtship and prespawning behavior occurs within the nest. The adhesive eggs are laid in a jelly-enclosed cluster on the ceiling of the spawning chamber. Ovariotomy of preserved gravid females from throughout the distributional range of *C. asper* yielded counts of 336 mature oöcytes in a 49.5-mm S.L. female, to 5,652 mature oöcytes in a female of 119.5 mm S.L. The largest female examined was 192 mm S.L., but she was spent. A conservative estimate of the number of mature oöcytes would be about 10,000 for this female. Numbers of viable eggs, in masses collected in the field, varied from 700 to 4,000 per cluster. However, one male may court and successfully mate with as many as 10 different females (personal observation). As many as 10 egg masses, in varying stages of development from newly-fertilized to near-hatching, have been found in the nest of a single brooding male. An estimated 25,000–30,000 eggs were present in this one nest.

After spawning, the spent females leave, or are chased from, the nests and they again aggregate above the spawning areas and begin feeding. The males remain in the nests, fanning and protecting the eggs, and do not eat until hatching of all egg clusters is completed. Much of the courtship and prespawning behavior, as well as most of the paternal brooding behavior through hatching, has been documented and will be reported elsewhere.

Laboratory studies on the behavior of *C. asper* larvae, done in extension of salinity-tolerance experiments (also to be reported elsewhere), indicate that at 12° C the larvae 5–7 mm in total length begin swimming immediately upon hatching. They remain pelagic, as lightly-pigmented transparent larvae, for a period of 30–35 days before metamorphosing and settling to the bottom.

Figure 5 illustrates numbers and distribution of *C. asper* young-of-the-year, 12–25 mm S.L., taken in a total of 700 seine hauls. In late spring and throughout the summer, the newly metamorphosed young-of-the-year are found in great numbers around and below the spawning site. The concentration is greatest around station C-1A, where there is a bed of fine, pea-size gravel adjacent to a large oyster bed. In mid-summer, there is a definite upstream migration of the young-of-the-year. In both 1960 and 1961, the increasing abundance of young-of-the-year at stations C-4 and C-5 was correlated with the decreasing abundance of specimens in the estuarine areas of the river (Fig. 5).

Spawning Period and Temperature Relationships

Egg clusters were collected from several localities in the lower Fraser Valley (cf. Fig. 1) and in the Little Campbell River. Gonads were examined in over 1,100 preserved museum specimens from all latitudes within the distributional range of *C. asper*. These data indicate that egg deposition begins in the south of the distribution range (low latitudes) in February, and progresses northward until late July. Males usually attain full reproductive maturity about a month before, and remain in spawning condition for almost a month after, the period of oviposition in females. Gravid females have been found over a 4-week period in Squakum Lake, and a 6-week period in the Little Campbell River. Ripe males have been taken over an 8–12 week period, respectively, in these same localities.

The earliest date on which a ripe male, in nuptial dress and with flowing sperm, was collected is February 6, in San Francisco Bay. The earliest collection of gravid females was in Waddell Creek, California, on February 24. In the north end of the range, gravid females were taken as late as June 20 in Petersen Creek, near Juneau, Alaska, and on July 22 in streams entering Juskatla Inlet, Queen Charlotte Islands. Gravid females have also been collected from Middle River, near Takla Lake, on June 28, and from Meziadin Lake, B. C., on July 25.

Field records and personal observations indi-
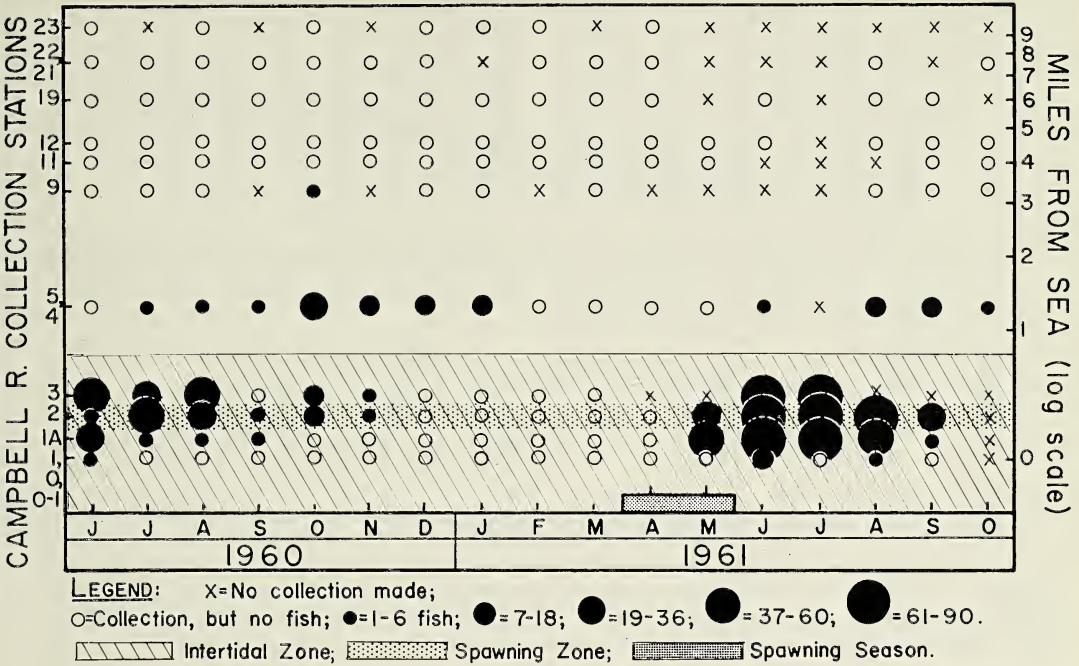
Fig. 5. Monthly distribution of young-of-the-year *Cottus asper* within the Little Campbell River. Data taken from pooled biweekly samples representing results of 700 seine hauls.

cate that natural spawning temperatures range from 8° to 13° C. Egg-rearing experiments at various temperatures resulted in complete mortality at 18° C, less than 50% survival at 15° C, and greater than 85% survival at 12° C. Control of lower temperatures was beyond the limitations of available equipment.

The annual mean range of ambient temperatures experienced by inland populations of *C. asper* is twice as great as that experienced by coastal populations at the same latitude (Krejsa, 1965:109). The monthly mean temperature range between northern and southern localities is from 8.8° to 19.5° C on the coast, and from 9.6° to 29.6° C inland. *A priori*, one might expect that inland populations would experience a greater range of developmental temperatures than do coastal populations. Apparently, however, they do not. When monthly mean temperatures, representing inland and coastal localities encompassing the distributional range of *C. asper*, are plotted against latitude, the mean temperature differences between inland and coastal localities during the spawning period are almost negligible (Fig. 6). In fact, the empirically determined, average spawning temperature

range of 8° to 13° C (shaded bar, Fig. 6) can be followed as a thermal "wave" progressing through inland and coastal localities from the south in February, to the north in June. Approximate spawning times, determined from examinations of gonadal condition in more than 1,100 specimens from all latitudes, are in general agreement with this south-north progression although the latitudinal range over which spawning occurs in March, April, and May is remarkably consistent (Fig. 6).

Theoretically, inland forms have a shorter period of exposure to spawning temperatures of 8° to 13° C than do coastal forms (Fig. 6). This supposition has been borne out by field data from the two most frequently collected spawning sites, Squakum Lake and Little Campbell River.

According to Figure 6, the inception of spawning in inland streams should lag behind that of coastal streams at similar latitudes. This is because upstream or inland areas remain colder for a longer period than do coastal areas. This is apparently true in the lower Fraser Valley. For example, the following localities are all within 15′ of 49° N, and gravid females and/
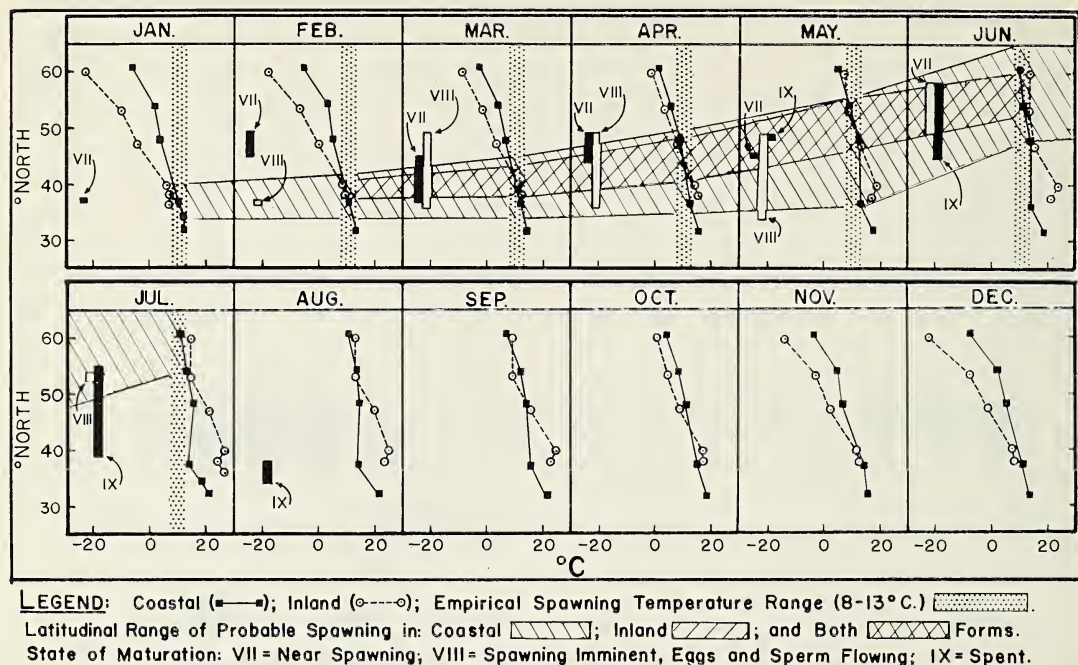
FIG. 6. Monthly mean temperatures in °C arranged by latitude for coastal and inland localities encompassing the distributional range of *Cottus asper*. Solid or unfilled vertical bars, left side of each panel, indicate actual ranges of latitude over which specimens have been found in a given state of maturity. Temperature values after Krejsa, (1965:109).

or eggs have been collected from them during the following dates: March 7 to May 10 in Little Campbell River (122° 46′ W); March 25 to April 15 in South Alouette River (122° 35′ W); and April 30 to May 27 in Squakum Lake (122° 00′ W).

DISCUSSION

The present study confirms the existence of a downstream spawning migration of the prickly sculpin in the Little Campbell River. It not only documents the occurrence of intertidal spawning in this coastal population of *C. asper,* but indicates that this spawning is successful. By extrapolation, the success of intertidal spawning in other coastal streams of the Pacific coast, where catadromous populations of *C. asper* have been reported, is indicated.

The lack of a seaward migration in "inland" populations with or without immediate access to the sea is also documented. In these populations, fresh-water spawning is the invariable norm.

Krejsa (1965) has discussed the evidence for recognizing a genetic distinction between "coastal" and "inland" populations of prickly sculpins based on morphology (prickling patterns) and geographic distribution. Bohn and Hoar (1965) have presented physiological evidence based on a comparison of iodine metabolism in "coastal" (Little Campbell River) and "inland" (Lagace Creek, Hatzic Lake) forms of *C. asper.* They concluded that the two populations studied have diverged genetically in their physiological capacities to deal with water of different electrolyte content.

If the above evidence is considered in light of the present study, the following picture emerges. Weakly-prickled *C. asper* living in coastal streams having open access to the sea undertake a downstream migration to the estuarine regions where eggs are spawned, hatched, and the young are reared successfully. Densely-prickled *C. asper* living in distant inland streams, where access to the sea is almost impossible, undertake only local migratory movements. But densely-prickled forms living in some inland

lakes and streams relatively close to the sea, where access to the sea is open and relatively easy to achieve, do not migrate seaward. They also undertake only local movements and spawn within the fresh-water system in which they are found. Such primary differences in behavior, correlated with distinct differences in prickling patterns, geographical distribution, and iodine metabolism, further corroborate the contention that "coastal" and "inland" forms of C. asper are genetically distinct.

Figure 5 shows a lag of about two months in the appearance of young-of-the-year C. asper, 12–25 mm S.L., after the first recorded spawning in March. Water temperatures in March are normally from 8° to 10° C. Eggs spawned early in March probably have an incubation period several days longer than the 15–16 day period found to be typical at 12° C in the laboratory. The lag shown in Figure 5 probably is due to an incubation period of 3 weeks followed by a pelagic larval stage of 4–5 weeks. Plankton tows taken during late April in the shallow back-eddies of the stream have captured a few larvae 9–10 mm S.L. (not recorded in Fig. 5).

An upstream migration of adults precedes that of the young-of-the-year in late summer. This is probably related to the food habits of the two groups and also to the fact that a later return of the young-of-the-year coincides with lower water levels in the stream, when reduced water velocity facilitates access upstream.

The usual spawning temperature range for C. asper is from 8° to 13° C. It is assumed that in most populations spawning is initiated within this 5° range of temperature, which proceeds in somewhat of a thermal "wave" from south to north in both inland and coastal localities (Fig. 6). This is not to say that they all spawn at the same temperature within the range. Furthermore, because the monthly rate of increase of ambient temperature is greater in the north, the duration of exposure of prickly sculpin eggs to any given temperature within the 5° C temperature range may be shorter. Eggs subjected to these conditions presumably would have a faster development than eggs which developed under relatively more thermostable conditions, such as occur in the south of the distributional range. Low meristic counts are gen-

erally (although not invariably) associated with faster rates of development. An experimental analysis of temperature-determined morphological differences is needed, especially of meristic differences, between "coastal" and "inland" populations of C. asper at the same latitude and between fishes from the north and south ends of their respective ranges. The implications and the desirability of such studies in determining the validity of the proposed genetic distinction between "inland" and "coastal" populations are obvious. The existing meristic evidence (Krejsa, 1965) is equivocal.

SUMMARY

1. The stream studied, the Little Campbell River, is a small coastal stream, the lower $\frac{1}{2}$ mile of which is subject to tidal inundation of mixohaline waters.

2. In late winter and early spring, the adults and juvenile prickly sculpins migrate downstream to the estuarine region of the Little Campbell River, the only region in the lower 4 miles in which suitable spawning substrate is available.

3. Males set up nesting sites under large cobbles and rocks, and courtship occurs both outside and within the nest.

4. Spawning occurs from March throughout early May.

5. Newly-hatched larvae begin swimming immediately and remain pelagic for a period of 30–35 days before metamorphosing and settling to the bottom.

6. In May, metamorphosed young-of-the-year (approximately 12 mm S.L.) begin appearing only in those collections taken in the estuarine portion of the river. They occur in great abundance until September, when the numbers decrease in the estuary and increase in upstream, nonestuarine waters.

7. During the nonmigratory phase of its life history, the prickly sculpin population in the Little Campbell River is distributed primarily in the low gradient, low velocity, portions of the stream.

8. Within any given population of prickly sculpins, the males are reproductively active longer, in a given season, than the females. The period of reproductive activity of both sexes is

more extensive in "coastal" populations than in "inland" populations.

9. The empirically determined, average natural spawning temperature of *C. asper* is from 8° to 13° C for both "coastal" and "inland" populations. Within this range of temperature, egg deposition begins in February in the south of the distributional range and progresses northward until July.

10. The existence of catadromous "coastal" populations and nonmigratory "inland" populations is indicative of genetic distinction between them. This contention is further strengthened by the existence of parallel differences in morphology, physiology, and geographic distribution.

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ADDENDUM

Since this manuscript was submitted for publication, Mr. Gerald D. Taylor has presented an excellent statistical analysis of experimental field and laboratory studies on the interrelationships of *Cottus asper* and *C. aleuticus* in the Little Campbell River.[1] His thesis forms a valuable contribution to our present knowledge of sculpin ecology. Most of his conclusions expand and elaborate upon many of the observations reported above. However, his study opens up the possibility that some of the prickly sculpins in the Little Campbell River do not spawn in the lower estuarine portion of the stream but upstream "in close proximity to spawning *C. aleuticus*."

In other nearby coastal streams where stream profiles are different, I have collected reproductively active *C. asper* and *C. aleuticus* in close proximity, but never have I done so in the Little Campbell River. I am skeptical of Taylor's statement primarily because his collections were carried out only during 5 months (of a 7-month period: August to November, 1965, and February, 1966), all of which are outside the normal spawning season of most *C. asper* as documented above. Taylor's study will be given more consideration in a future report on the behavior of *C. asper* and *C. aleuticus*.

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[1] Taylor, G. D. 1966. Distribution and Habitat Responses of the Coastrange Sculpin (*Cottus aleuticus*) and Prickly Sculpin (*Cottus asper*) in the Little Campbell River, British Columbia. Unpublished M.S. thesis, Department of Zoology, University of British Columbia (December, 1966).

Herpetofauna of the Hawaiian Islands[1]

✓ DON HUNSAKER II[2] and PAUL BREESE[3]

THIS STUDY was undertaken to determine the changes that have occurred in the herpetofauna of the Hawaiian Islands since the work in the early forties by Oliver and Shaw (1953). The work is a result of a field survey of most of the islands conducted by the authors during the summer of 1962. Since the purpose of the survey was to observe gecko vocalization, more data are available on this group than on the others. The islands afford a unique opportunity to observe a dynamic fauna since there are constant introductions from foreign sources. Periodical surveys have been made which furnish an investigator a well annotated history. Changes have been observed during each of the major surveys, made by Stejneger (1899), Snyder (1917), and Oliver and Shaw (1953).

In an accurate analysis of the faunal characteristics of the islands during 1943 when their study was conducted, Oliver and Shaw (1953), listed 8 species of amphibians and 15 species of reptiles. Since that time the house gecko, *Hemidactylus frenatus,* has been introduced. Two iguanid lizards, the Cuban anole, *Anolis porcatus,* and the horned lizard, *Phrynosoma cornutum,* have become established and are now considered to be permanent residents of the islands. *Anolis* was established by 1951 (Shaw and Breese, 1951) and *Phrynosoma* since that time. Hawaii's laws prohibit introduction of any snakes, but occasional specimens have been collected. Gopher snakes, *Pituophis catenifer,* and garter snakes, *Thamnophis elegans,* have been collected on Oahu, but are not considered to be established. These probably represent pets that have escaped and at the present time do not constitute a significant part of the fauna.

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REPTILIA
SERPENTES (SNAKES)

Blind Snake (Typhlops braminus)

About 1930 this species was accidentally introduced on the island of Oahu with a shipment of palm trees from the Philippines which were planted around the new Kamehameha Schools in Kapalama, Honolulu. It became established quickly in the vicinity of the schools, and during the following decade spread into the residential areas of Honolulu. By 1947, it had been collected in an area several miles from the original locality (Fisher, 1948), and it now appears to occupy the lowland area over the entire island. It is unknown on the higher mountains, but this may be due to inadequate collecting efforts. The large amounts of top soil that are transported from one part of the island to another probably are responsible for the spread of this fossorial animal. Recently, *Typhlops braminus* has been collected in Kahului, the major port city of the island of Maui. While there are some restrictions on the transportation of soil around vegetation or domestic plants between the islands, certain people manage to evade them. Such shifting of top soil, potted plants, etc., as well as large-scale freight shipping by sea, probably is responsible for the introduction of the blind snake on Maui. Its establishment on the other islands is to be expected.

SAURIA (LIZARDS)
GEKKONIDAE

Mourning Gecko (Lepidodactylus lugubris)

The first Hawaiians probably introduced this species during early population invasions approximately 1,000 years ago. The eggs are highly adhesive and can be seen clinging to mats and other household articles such as early immigrants probably brought with them. They have been recorded in the Panama Canal Zone

by Smith and Grant (1961), undoubtedly in-
troduced by this method of egg transport. Today
the species is found throughout the islands,
from remote forests to the downtown areas of
the largest cities. It is the most frequently ob-
served lizard and is well represented in collec-
tions because of its gregarious habits, little fear
of humans, and population concentration in
areas inhabited by people. This common gecko
apparently has adapted itself with great success
to living in close association with humans. It is
a common observation that these geckos occur
in greater numbers in well populated areas than
in more remote sections. Of a series of 21 indi-
viduals collected in a transect from an uninhab-
ited area into a city, 10 were collected in a pop-
ulous section, 5 from the fringe area, and 6
from the uninhabited area. In making this tran-
sect an attempt was made to maintain a con-
stant unit of effort in each of the three habitats
during the collections. The great number of
numerous species of nocturnal insects attracted
by the electric lights of the city probably is re-
sponsible, in large part, for the large gecko
population in the city. This does not explain,
however, the abundance of geckos in or near
man-made structures that were remote from any
lighted areas. In nonurban areas, they are defi-
nitely associated with open forests rather than
with densely forested areas.

Observations of several individuals indicate
that *L. lugubris* is rather sedentary and that the
home range usually does not exceed an area of
6 or 8 ft in diameter. However, these lizards
periodically migrate from one area to another.
These movements are not a coordinated group
effort, but appear to be a simultaneous evacua-
tion of the normal home ranges of many indi-
viduals. During these periods, individual geckos
have been seen moving across walls, down tree
trunks, over sidewalks, etc. Such periods of ex-
cessive activity have not been correlated with
season, rainfall, temperature, or other factors.

L. lugubris is active from shortly before dark
until sunrise. Although highly gregarious, they
show some aggression toward each other. A
chirping noise is utilized in social behavior and
a squeaking occurs during painful or aggressive
encounters. Tail-waving has been observed in
social interactions. The females are slightly
larger than the males. The mean snout–vent

length of 26 females was 41.69 mm, ranging
from 33.0 to 46.7 mm. The mean snout–vent
length of 7 males was 35.96 mm, ranging from
32.2 to 42.4 mm.

Tree Gecko (Hemiphyllodactylus typus typus)

No significant changes have appeared in the
density and distribution of this species since
1943; it remains rather rare. Of 161 geckos
collected in Kailua on Oahu, only 5 were of this
species; 4 of them were collected on the sides
of buildings in the city and 1 from under the
bark on a tree. They are extremely agile and
wary lizards and it is much easier to collect
them from the sides of buildings than from
tree trunks. Hence we do not believe that our
larger collection from the city buildings neces-
sarily implies a larger population there.

H. typus typus is not a gregarious species;
only 1 individual was collected from a well-
lighted building which supported over 80 other
geckos. On a darkened building about 30 ft
away, 2 other individuals were collected about
10 ft apart. The only lizard found in close
association with the tree gecko was the house
gecko.

House Gecko (Hemidactylus frenatus)

This species is the latest addition to the her-
petofauna of the Hawaiian Islands (Hunsaker,
1966). It was first observed in June 1951 in
the city of Kailua, about 20 miles north of
Honolulu. It is well established at the present
time and appears to be rapidly replacing both
Hemidactylus garnoti and *Lepidodactylus lugu-
bris* in the cities on Oahu. *H. frenatus* can be
identified easily by the series of enlarged scales
which encircle the tail, exhibiting concentric
circles of short spines (Fig. 1). These circles
are separated by normal scales. This species has
a cylindrical tail and lacks the lateral folds and
loose femoral skin of *H. garnoti*. *H. frenatus* is
very similar to the fox gecko in size and color,
but it is much more aggressive. Not uncom-
monly it attempted to bite the collector.

Mixed colonies of *H. garnoti* and *H. frenatus*
are rare. Apparently the new immigrant is much
more successful a competitor than are the other
species of geckos. This factor, and its greater
aggressiveness, apparently are responsible for its
rapid replacement of the fox gecko in urban
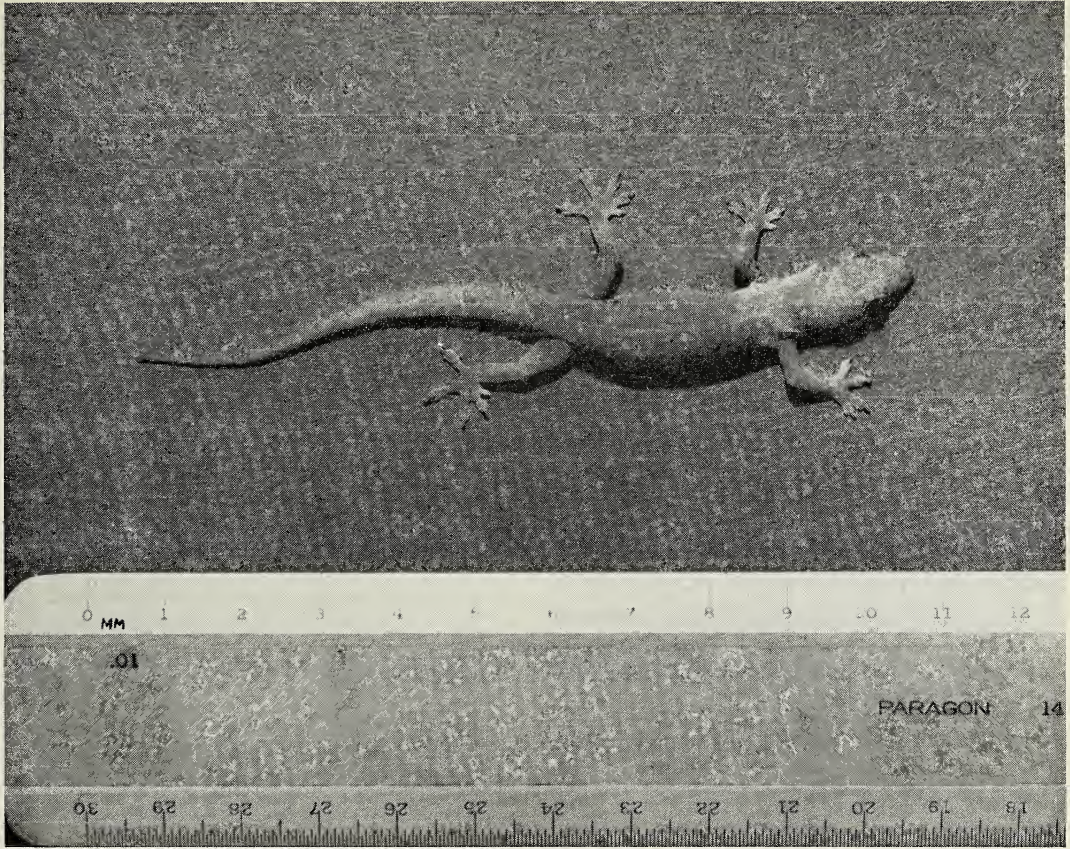
FIG. 1. *Hemidactylus frenatus.*

areas. *H. frenatus* has not been collected in areas removed from human habitation. In a transect which extended from an uninhabited area into the city of Kailua, 5 *H. garnoti* were collected in the uninhabited area and only 1 in the city proper. Conversely, 40 *H. frenatus* were collected in the city and none in the peripheral areas. Very few mourning geckos were found to be associated with *H. frenatus.* In Kuala Lumpur, Malaya, *H. frenatus* is quite common in the inhabited areas and *L. lugubris* is much more difficult to collect in the fringe areas. In the past, the well-lighted residential areas of Honolulu have been occupied by *L. lugubris* and the invasion of this habitat corresponds with findings of Church and Lim (1961), who stated that in Bandung, Java, *H. frenatus* preferred residential areas which were well-lighted and damp. In an area that has been under observation for the past few years, the disappearance of the fox gecko and the mourning gecko popula-

tion coincided with the appearance of this species. These large geckos appear to have a home range of an area about 12–15 ft in diameter. They are highly vocal and a distinctive series of five or six call notes can be heard up to 100 ft away. Aggressive or painful situations may provoke a prolonged squeak. This species occurred in close association with the stump-toed gecko (*Peropus mutilatus*). *H. frenatus* were observed in Kailua, in many parts of Honolulu, around the International Airport, and in the wharf area. Four individuals of this species were collected only in the harbor areas of Kahului on Maui, while *H. garnoti* and *L. lugubris* were collected in other sections of the city. This distribution indicates that *H. frenatus* has arrived only recently on Maui. None of these lizards has been collected on any other island. This is a large species; the largest individual collected was a male 58 mm in snout–vent length.

The current distribution of *H. frenatus* indi-

cates that it is quite successful in establishing itself in new areas. The species is very widespread in the Orient and in the Malay States. Grant (1957) recorded it from Acapulco, Mexico; Tanner on Saipan in 1948; in 1950 it was recorded from Morotai; Church and Lim (1961) recorded it in Java; Larry Richards collected it from Guam in 1947. In all probability representatives of the Mexico population were transported by early traders, and the recent range expansion is due to equipment and material shipped during World War II.

Fox Gecko (Hemidactylus garnoti)

The future of this species in the islands will be interesting to follow. At the present time it is uncertain whether *H. frenatus* is replacing this species in unpopulated areas. If the fox gecko is better adapted to living in forested areas, it will probably continue its existence in this habitat. If the house gecko is as efficient in displacing the fox gecko in remote areas as it is in the cities, the future of this long-term resident is questionable. The fox geckos have been established for many years and probably are one of the earliest inhabitants of the islands. In Malaya, there are areas where both *H. garnoti* and *H. frenatus* live in close association, and so it is possible that the two species will continue to be sympatric in Hawaii's fauna.

Of 12 eggs from the island of Hawaii which were laid during the last week of June, the largest was 17.0 × 8.9 mm, the smallest 9.4 × 8.7 mm. These measurements compare well with those of eggs of the same species recorded by Cagle (1946) for eggs from a population on Tinian (which had a mean of 12 × 7 mm). Measurements made 2 weeks later did not indicate a significant change in size. Of the 12 eggs 7 hatched, and the mean snout-vent length of the newborn lizards was 24.08 mm, the mean total length, 48.0 mm. The range of snout-vent length was 26.0–22.5 mm; the range of total length was 51.0–45.5 mm. These measurements are well within the range quoted by Snyder (1917) for Hawaiian populations: 39.5–56.0 mm total length.

The maximum incubation period for eggs laid in Hawaii and hatched at room temperature (74°F) was 64 days. Cagle (1946) hatched a series of eggs of this species in a 45-day incubation period.

Stump-Toed Gecko (Peropus mutilatus)

There appears to be no significant change in the distribution of this gecko. It occurs in rather dense populations in some areas and is scarce in others. It is found away from the city of Honolulu in the back country and is quite common at the International Airport on Oahu. Females are slightly larger than the males. In a series of 17 females measured, the mean snout-vent length was 45.60 mm, with a range of 39.5–55.5 mm; for 34 males, the mean snout-vent length was 43.65 mm, with a range of 29.0–57.5 mm.

IGUANIDAE

Gray Cuban Anole (Anolis porcatus)

This species is well established on Oahu at the present time. Both large adults and immature forms are commonly seen in Honolulu. The original site of collection was in the Kaimuki section of Honolulu. It has spread to other nearby sections of the city and to Manoa Valley, and is presently established on the north side of the island, at Kailua. The first introductions were probably imported pet lizards which escaped. We can consider this species to be a permanent member of the fauna of Oahu. It has not been collected from the other islands.

Texas Horned Lizard (Phynosoma cornutum)

An increasing number of reports and of specimens collected indicate that this species is probably established as a permanent resident of the Hawaiian fauna on the island of Oahu. These animals undoubtedly originated from escaped pets. They have been found from the slopes of Diamond Head throughout Honolulu to the xeric areas above Pearl Harbor. No concrete evidence has been obtained to indicate that a reproducing colony has been established, with eggs and hatchling lizards. Probably this lizard is reproducing, since immature specimens have been obtained from the islands, and the 10 or 15 reported is an unusually high

number to be accounted for by the escape of pet lizards.

SCINCIDAE

Snake-Eyed Skink (Ablepharus boutoni poecilopleurus)

No important changes have occurred in the population of this species. It is still rather common in some of the more arid sections, but it occurs in definitely localized populations. In some areas it is absent, although the environment is similar to that of other areas where the skink is common.

Moth Skink (Lygosoma noctua noctua)

At the present time, the moth skink is found only in a small area on the northern coast of Oahu, near Kahuku Point. There seems to be little doubt that the rapid expansion of *Lygosoma metallicum* is responsible for the decrease in the once large populations of the moth skink. The area in which it now occurs is similar to large areas of Oahu which are now occupied by the metallic skink and at one time were occupied by *L. noctua*. The increase in amount of land under cultivation has not been great enough to account for the reduction that has been observed. No data are available for populations once observed on Hawaii, Kauai, and Maui.

Metallic Skink (Lygosoma metallicum)

Few animals have been so successfully introduced as was the metallic skink on the island of Oahu. Its rapid multiplication on this island has produced remarkable numbers in the lower areas. It is aggressive with individuals of the moth skink, and it is certainly unafraid of humans. The success of the species probably is due in part to its apparent lack of fear of humans. It is easy to approach these lizards, and they can be found close to human habitations. The species is still known only from Oahu.

AMPHIBIA

Gold and Black Poison Frog (Dendrobates auratus)

This frog has been limited in its distribution only to the sites where it was released.

It was originally introduced in upper Manoa Valley in 1932. This site now has a well-established population of frogs which extends to lower parts of the valley during the rainy season. Additional plantings with subsequent establishment have been made in Waiahole Valley, and the population has been observed to fluctuate in size at this locality, again according to the amount of water available.

Bull Frog (Rana catesbeiana)

This frog is extremely prolific and is well established on all major islands. No major changes in the populations have appeared since the 1940s.

Green Frog (Rana clamitans)

Since its introduction on Oahu in 1935, no great expansion of the population has been evident. It is not common anywhere on Oahu and has not been reported on other islands.

Wrinkled Frog (Rana rugosa)

This species is well established and is quite common in some areas. The population size varies with the amount of rainfall available. During 1962 the populations of most amphibians were reduced to half the numbers found in 1961, when surface water was much more plentiful.

Marine Toad (Bufo marinus)

This species is found on all the major islands and is the commonest species of amphibian.

SUMMARY

A survey of the herpetofauna of the Hawaiian Islands was conducted during 1962 to determine any changes that might have occurred in the previous 20 years. New faunal species which have become established are *Anolis porcatus*, introduced in the late 1940s; *Phrynosoma coronutum*, introduced about 1955; and *Hemidactylus frenatus*, first observed in July 1961.

Other species have extended or contracted their ranges, but no other significant changes were observed. It was noted that populational variations in amphibians could be attributed to annual changes in available surface moisture.

The house gecko, *Hemidactylus frenatus*, is rapidly increasing in numbers and is apparently being introduced into the other islands from Oahu. The most important means of introduction appears to be by the movement of boat cargoes from one harbor to another.

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NOTES

Note on the Distribution of *Euphausia eximia* and *E. gibboides* in the Equatorial Pacific

Claude Roger[1]

The material here considered was collected during the Alizé cruise of the R.V. "Coriolis" from the Centre O.R.S.T.O.M. Noumea. The Alizé collections extended from 92°20′W to 162°45′E along the equator. The samples were taken with a 5-ft Isaacs-Kidd midwater trawl, towed obliquely from a depth of 300 m to the surface.

GENERAL RESULTS

The distributions of the whole euphausiid fauna will be discussed in detail in a further publication. At present they appear to be not far different from those described by Brinton (1962); however, two features become evident:

1. There is an evolution of the specific composition of the euphausiid fauna from east to west.

2. Two species among the most important ones, *Euphausia eximia* Hansen and *E. gibboides* Ortmann, have been caught not only in the eastern equatorial Pacific as previously recorded (Brinton, 1962), but also in the Central Pacific, as far westward as 164°15′W and 148°07′W, respectively. The present note deals with the occurrence of these two species in Central Pacific waters.

DISTRIBUTION OF *Euphausia eximia*

Table 1 lists the stations at which *E. eximia* were taken.

According to Brinton (1962), the farthest westward record for this species is 118°W in the South Equatorial Current (2°N–2°S) and 145°W at 10°N. During the Alizé expedition,

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TABLE 1

QUANTITATIVE DISTRIBUTION OF
E. eximia AND *E. gibboides*

STATIONS	NUMBER PER STANDARD HAUL* *E. eximia*	*E. gibboides*
0.50S, 92.20W	752	316
0.49S, 95.28W	416	58
0.53S, 98.18W	6,224	272
1.00S, 101.14W	780	36
0.16S, 103.48W	2,856	256
0.05S, 106.45W	2,136	96
0.40S, 109.10W	1,233	33
0.20S, 115.40W	896	7
0.03N, 118.27W	585	24
0.00 120.45W	933	45
0.40S, 123.35W	1,330	0
0.40S, 125.53W	558	16
0.33S, 128.26W	183	5
0.19S ,131.42W	40	5
0.33S, 134.46W	277	4
0.17S, 137.45W	17	3
0.01N, 145.06W	0	0
0.14S, 148.07W	0	1
0.27S, 151.15W	0	0
0.28S, 154.38W	0	0
0.38S, 158.10W	0	0
0.22S, 161.06W	1	0
0.20S, 164.15W	2	0
0.23S, 167.30W	0	0
0.28S, 170.30W	0	0
0.23S, 174.10W	0	0
0.20S, 177.30W	0	0
0.23S, 179.00E	0	0
0.27S, 176.05E	0	0
0.12S, 172.30E	0	0
0.18S, 169.00E	0	0
0.30S, 166.00E	0	0
0.38S, 162.45E	0	0

* Length of the column of water filtered: 5000 m.

three specimens were caught at 164°15′W and 161°06′W, about 2,700 miles farther west.

E. eximia seems very common at 135°00′W, and very abundant east of 126°W. From 92° 20′W (beginning of the cruise) to 137°45′W

this species accounts for 50–90% of the whole euphausiid material.

On the other hand, it must be pointed out that, in a number of individuals, the inner protuberance of the anterior margin of the second segment of the first antennal peduncle is trifurcate (Fig. 1) and not simple or bifurcate as usually described (Hansen, 1912; Boden, Johnson, and Brinton, 1955). In some specimens, this protuberance presents four spines (Fig. 2).

DISTRIBUTION OF *Euphausia gibboides*

This species was present more in the west than was previously known (see Table 1).

The farthest westward that a specimen of *E. gibboides* was collected during the Alizé cruise was 148°07'W. This record extends the westward limit of distribution, recorded previously as 132°W (Brinton, 1962).

The species is present between 148°07'W and 126°W, rather common between 126°W and 109°10'W, and common between 109°10'W and 92°20'W (beginning of the cruise).

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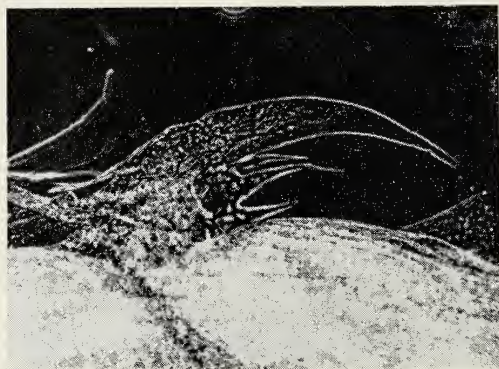
FIG. 1. *E. eximia.* Protuberances of the distal end of the second segment of the first antennal peduncle. *Foreground*: outer protuberance (simple). *Background*: inner protuberance (trifurcate); on the *right*, beginning of the dorsal keel of the third segment.
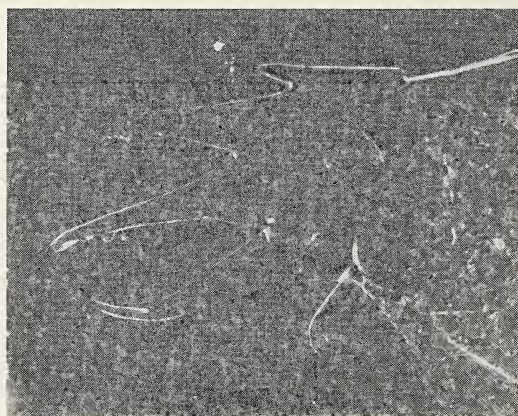
FIG. 2. *E. eximia.* Inner protuberance of the distal end of the second segment of the first antennal peduncle, showing four spine-shaped denticles.

Monobrachium parasitum, a One-Tentacled Hydroid, Collected at Vancouver Island

Richard D. Campbell[1]

THE COLONIAL HYDROID *Monobrachium parasitum* (Mereschowsky) is of interest to systematic and developmental biologists because of its peculiar form and its commensal habitat. Each feeding polyp has only a single tentacle, and the colony grows and develops a characteristic polymorphic pattern on living bivalves (Wagner, 1890; Hand, 1957). This note reports the rapid collection of this unusual hydroid without heavy equipment.

On August 16, 1964, 13 colonies of *M. parasitum* were collected at Fraser's (1918) original locality in Nanoose Bay, Vancouver Island, British Columbia. Nanoose Bay is about 1 km wide and 3 km long, and opens eastward. Water turnover is extensive during tidal changes. Tidal currents are located predominantly along the northern shore. Accordingly, the bottom of the northern third of the bay is composed of sand and light gravel, with remains of broken shells. The southern two-thirds presents a graded bottom from fine sand centrally to mud along the shallow southern shore. The bivalve *Axinopsis* was collected with a 1-mm mesh conical net 2 inches in diameter, towed for 10 minutes behind a small boat. *Monobrachium* colonies were found in three out of seven tows made in the central third of the bay (124° 9.2′ W, 49°

15.8′ N, 16–17 fathoms), but not in either the deeper northern or the shallower southern sides.

Axinopsis with *Monobrachium* which were brought into the laboratory showed rapid and extensive burrowing through fine sand. Generally the hydroids were completely under the surface of the sand. No colonies showed any evidence of reproductive polyps or of medusa buds.

Hand (1957) found *Monobrachium* in a number of dredge loads from the California and Baja California coast. Besides Hand, only Fraser (1918) had reported *Monobrachium* from the West Coast of North America. Repeated dredgings in the San Juan Archipelago, Washington, failed to reveal any specimens, even in habitats similar to those prevailing on the east coast of Vancouver Island.

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[1] Friday Harbor Laboratories, San Juan Island, Washington. Present address: Department of Organismic Biology, University of California, Irvine, California 92664. Manuscript received July 23, 1966.

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Crawford, David L. 1920*a.* New or interesting Psyllidae of the Pacific Coast (Homop.). Proc. Hawaii. Ent. Soc. 4(1):12–14.

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PACIFIC SCIENCE

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CONTENTS

CONTENTS (*continued*)

On the Surface Swarming of Euphausiid Crustaceans[1]

Yuzo Komaki[2]

ABSTRACT: A general aspect of the daytime surface swarming of *Euphausia pacifica* in Japanese nearshore waters is described in connection with the water temperature. Swarming usually starts with a local minimum temperature around 7°C and terminates with a temperature just below 16°C. The swarming season is essentially in spring, from February through May, with little difference among regions. The main swarming areas are on the Pacific coast around Kinkazan, and on the coast of the Sea of Japan around Sadogashima, in Wakasawan and its vicinity, around Oki, and on the east side of the Tsushima Gunto.

It is shown that the swarming is closely related to cold water masses, and that the approach of offshore cold water masses to the nearshore areas and the mixing process in the coastal areas may provide favorable conditions for swarming. Swarming of *E. pacifica* is a phenomenon that occurs at the margins of the cold water bodies, and is related to the seasonal change in the geographical distribution of those euphausiids.

A uniformly low water temperature profile must be the necessary condition for swarming, but other possible factors stimulating euphausiids to swarm are enumerated.

It has been reported frequently from various parts of the world that conspicuous daytime aggregation of euphausiids takes place at the surface in rather nearshore waters (Table 1). The animals swarm in such large numbers that the sea surface turns red or brownish-red from their red and/or orange pigments. This phenomenon, as Bigelow (1926) pointed out, differs from their usual vertical migratory behavior because it occurs in the daytime, independent of the light intensity.

Most previous reports on this peculiar behavior of euphausiids have been descriptive, and very few observations have been made on its relationship to environmental factors. This may be attributed not only to the complexity of animal behavior in general, but also to the capriciousness of such phenomena. As is the

case with red tides, the surface swarming of euphausiids is not predictable from physical measurements.

Such a swarming phenomenon with *Euphausia pacifica* occurs in the nearshore waters surrounding Japan. A fishery based on *E. pacifica* is maintained in certain areas—around Kinkazan (Komaki, 1957), in Wakasawan Bay and vicinity, and along the coast of northwestern Kyushu. The local fishermen scoop *E. pacifica* swarming at the surface with a pyramid-shaped net. The surface swarming of euphausiids is regarded as sporadic, but the existence of the euphausiid fishery means that the surface swarming of *E. pacifica* must be at least an ordinary annual phenomenon.

While participating in the Survey of the Warm Tsushima Current and Related Waters during the period from 1953 to 1958, the author carried out ecological studies on euphausiids and reported briefly on the relationship between water temperature and the swarming of *E. pacifica* (Komaki and Matsue, 1958). The present paper emphasizes this relationship more extensively, employing additional data, information, and references.

TABLE 1
REPRESENTATIVE REPORTS ON EUPHAUSIID SWARMING

REFERENCE	SPECIES*	REGION	SEASON
Smith (1879)	*M. norvegica*	Eastport area	autumn
Murray (1888)	*M. norvegica*	Loch Fyne, Scotland	
H. F. Moore (1898)	*Thysanopoda* spp.	Eastport area	summer, fall
Lo Bianco (1902)	*M. norvegica*	around Capri I.	Feb., June, July 1901
Bigelow (1926)	*M. norvegica* *T. raschii* *T. inermis*	Gulf of Maine	spring–fall
MacDonald (1927)	*M. norvegica*	Oslo Fjord	fall, early winter
Hjord and Ruud (1929)	*M. norvegica*	off Møre, Norway	spring–fall
Hardy and Gunther (1935)	*E. superba*	S. Georgia waters	Nov.–Feb.
Fish and Johnson (1937)	*Thysanoëssa* spp.	Bay of Fundy	
Manteufel (1938, 1941)	*T. inermis*	Barents Sea	winter–spring
Mossentzova (1939)		Barents Sea	spring
Dakin and Colefax (1940)	*N. australis*	Sydney area	Sept. 1938
Einarsson (1945)	*M. norvegica* *Thysanoëssa* spp.	N. Atlantic	spring–summer
Gunther (1949)	*E. superba*	S. Georgia waters	Jan. 1937
Uda (1952)	*E. pacifica*	southern part of Sea of Japan	Feb.–May 1948
Sheard (1953)	*N. australis* *T. gregaria*	S. Australia, Bass Strait, S. Victoria, N. Tasmania waters	breeding season
Fisher et al. (1953)	*M. norvegica*	Monaco coasts	Aug. 1951 Jan. 1952
Boden et al. (1955)	*T. spinifera*	La Jolla coasts	June 1948
Peters (1955)	*E. superba*	Bouvet area in Antarctic waters	December
Komaki (1957)	*E. pacifica*	around Kinkazan	Feb.–May
Komaki and Matsue (1958)	*E. pacifica*	Japanese waters	Feb.–May
Ponomareva (1955, 1959, 1963)	*T. longipes* *T. inermis* *T. raschii* *E. pacifica*	northern part of Sea of Japan, N. Pacific	Mar.–June
Zelickman (1961)	*T. inermis* *T. raschii*	Murman coasts	Mar.–July
Brinton (1962b)	*E. pacifica*	north of Pt. Conception	Apr. 1956
Marr (1962)†	*E. superba*	S. Georgia waters	

* Abbreviations of genus names: *E.* = *Euphausia,* *M.* = *Meganyctiphanes,* *N.* = *Nyctiphanes,* *T.* = *Thysanoëssa.*
† Review of surface swarming of *E. superba* in Antarctic waters.

SOURCES OF INFORMATION

Swarming

Because of the infrequency of swarming of euphausiids in the Sea of Japan since 1953, direct observation of the phenomenon was not possible, but valuable information on the local swarming of euphausiids was obtained from fishermen. Fishermen are the best, most frequent, and most experienced observers of phenomena occurring in their favorite fishing grounds. From 1954 to 1956, a questionnaire was sent three times to more than 800 local fishermen's unions, which are scattered along
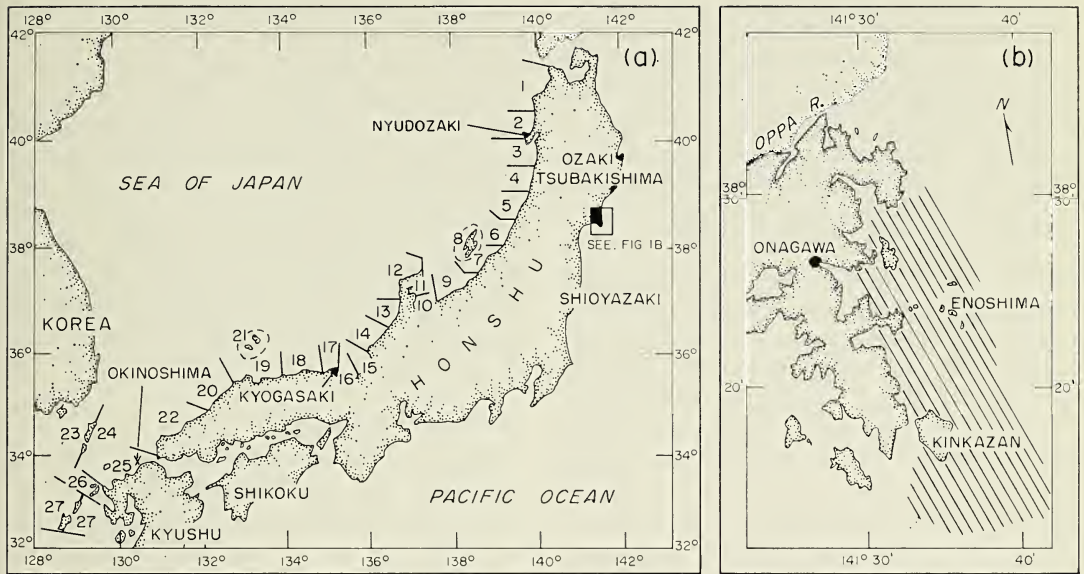
FIG. 1. (*a*), Map showing partition of coastal areas of the Sea of Japan into 27 zones in order to observe the regional differences in euphausiid swarming. Zones 15 and 16 cover the Wakasawan area. (*b*), Fishing ground (shaded area) of *Euphausia pacifica* in the vicinity of Kinkazan.

the coasts of Honshu, Kyushu, and adjoining small islands facing the Sea of Japan.

The rate of response to the questionnaire was approximately 30%. To facilitate analysis of the replies, the coastline of the Sea of Japan was partitioned into 27 zones of 0.5° latitude or according to geographical features of the coasts (Fig. 1*a*). The fishermen's unions were divided into 27 groups corresponding to these zones, so that geographical differences in the swarming, if any, could be detected. There were many responses suggesting interesting relationships between the swarming and environmental factors (hydrographical, meteorological, biological, and so on). The author interviewed fishermen from important regions, on the basis of the results of the questionnaire, such as the Wakasawan area. Information that could be treated numerically (at least to some extent) was employed in the present paper.

It was learned that, along the Pacific coast, the area around Kinkazan (Fig. 1*b*) is the only place where the relatively stationary swarming is observed every year and the euphausiid fishery is maintained. The author visited this area in every swarming season and participated in the euphausiid fishing operation in order to make direct observations. No written question-

naires were employed there. Reliable quantitative records of euphausiids fished from the Kinkazan district since 1953 were obtained from the fish market in Onagawa where almost all the euphausiids from this fishing ground were landed, but no similar numerical data on the yield of euphausiids were available from the Sea of Japan.

Water Temperature

Among the important environmental factors governing distribution and behavior of the organisms, water temperature is not only the most important factor, but also is the one for which data can be obtained most easily. Accordingly, these data were sought from the files of the hydrometeorological observations made by the various maritime and fisheries agencies listed below:

Federation of Fishermen's Unions of Miyagi Prefecture, Onagawa Branch. 1953–1959. Fisheries Statistics.

Fukushima Prefecture, Fisheries Experimental Station. 1956. Data on oceanographic observations off Fukushima Prefecture, 1914–1939.

Imperial Fisheries Research Office, Central Laboratory. 1915–1950. Data on oceanographic surveys in the surrounding areas of Japan.

Iwate Prefecture, Fisheries Experimental Station.

1954–1956. Data on oceanographic observations off Iwate Prefecture.

Japan Sea Regional Fisheries Research Laboratory. 1953–1959. Monthly report on the out-lined sea conditions of the Sea of Japan.

Ministry of Agriculture and Forestry, Section of Statistics. 1946–1956. Fisheries Statistics.

Miyagi Prefecture, Fisheries Experimental Station. 1910–1959. Records of hydrometeorological observations at Enoshima, Miyagi Prefecture.

Plankton Samples Collected in the Sea of Japan

Thousands of plankton samples were collected during the period 1953–1958 by various institutions that participated in the Survey of the Warm Tsushima Current and Related Waters. Most samples were collected in a strip within 100 miles of the coastline. The selected samples were examined for the purpose of ecological studies on euphausiids, and they were very useful in the confirmation of euphausiid species composing surface swarms.

<center>RESULTS</center>

The Species

Examination of specimens landed at the Onagawa fish market revealed that the euphausiids swarming in the Kinkazan waters were large specimens of *Euphausia pacifica* (longer than 20 mm from the tip of the rostrum to the end of the telson). Throughout four fishing seasons, only one stray specimen of *Nematoscelis difficilis* was found among the catches of huge quantities of *E. pacifica*. Combined swarmings of more than two species, such as those reported by H. F. Moore (1898), Fish and Johnson (1937), and Zelickman (1961), were not encountered in the Kinkazan waters.

The following five species of euphausiids inhabit the Sea of Japan (Ponomareva, 1955; Komaki and Matsue, 1958): *E. pacifica, Thysanoëssa raschii, T. inermis, T. longipes,* and *Pseudeuphausia latifrons*.

Plankton samples collected during the survey showed that *E. pacifica* and *P. latifrons* could be obtained from the areas within 100 miles from the coast. *Thysanoëssa* spp. never have been collected from that area, although Ponomareva (1959, 1963) has reported that the three *Thysanoëssa* species mentioned appear at the surface, forming remarkably dense swarms in the northernmost part of the Sea of Japan. *P. latifrons* is a small, warm-water form, shorter than 10 mm in total length (Hansen, 1916; Brinton, 1962*a*), and apparently it penetrates into the southernmost part of the Sea of Japan from the Tsushima Kaikyo only during summer and fall (Komaki and Matsue, 1958). Samples from surface swarms of a few occasions revealed that the swarms were composed of large *E. pacifica* only. Thus, *E. pacifica* must be the species composing the surface swarms in the nearshore waters of the Sea of Japan.

Features of Swarming

Hardy and Gunther (1935) have described beautifully the swarming behavior of *E. superba* at the surface, and their descriptions can be exactly applied to the surface patches of *E. pacifica*. The animals swim as close as 1–2 cm from each other, orienting themselves in one direction as if commanded by a leader. The swarms look like formless clouds, and frequently change in shape. They are red, brownish-red, or pale brown in color, depending upon their distance from the surface.

When participating in euphausiid fishing operations in the Kinkazan waters, the author found that swarming took place intensively at intervals of a few days. As shown in Figure 2, the daily landings of *E. pacifica* at the Onagawa fish market fluctuate with a pulselike rhythm. Inasmuch as only surface patches of euphausiids are harvested because of the fishing method, the landing on a given day is probably related to the standing crop of euphausiids swarming at the surface on that day. Daily catch per unit of fishing effort is the most suitable term to use in discussing such a fluctuation of standing crop, but data indicating fishing effort were not available. Fishing boats unload their catches at the market two or three times a day while euphausiids are abundant. Accordingly, the *aggregate* numbers of fishing boats in Figure 2 change approximately in parallel with the landings of euphausiids.

Efforts were made to relate this pulselike occurrence of swarming to the environmental factors that vary within short periods, e.g., irradiation, wind direction and intensity, and
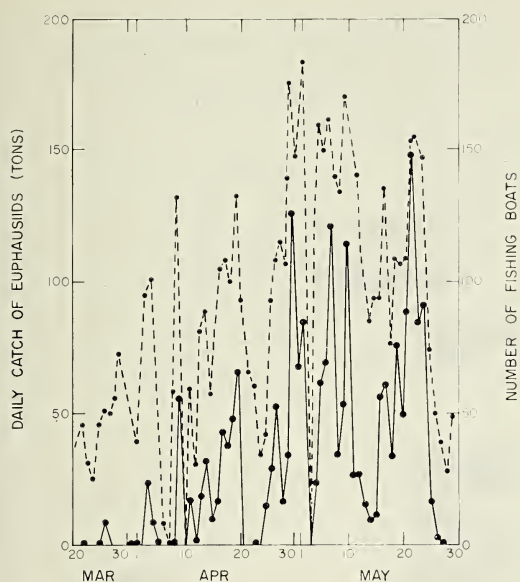
FIG. 2. Daily landings of *Euphausia pacifica* (*solid line*) from Kinkazan waters and daily change of aggregate number of fishing boats (*dashed line*) yielding euphausiids (1959).

the like, but there were no apparent relationships. The yield on a calm day is likely to be more abundant than that on a rough day, but this is caused essentially by the relative difficulty of the fishing operation. The time of swarming throughout a given day is not definite. It occurs in early morning on some days, while on other days it takes place in the afternoon even in bright sunshine.

Swarming Season

The fishing season of euphausiids corresponds with the swarming season in the area where the euphausiid fishery is carried out. As shown in Figure 2, the swarming season during 1959 in the Kinkazan waters started in the middle of March and terminated at the end of May. The season, however, changes slightly from year to year. The swarming season in the Kinkazan waters ranges between late February and late May in maximum extent.

Figure 3 shows the general aspect of the swarming season along the coasts of the Sea of Japan. The rectangles in Figure 3 show the range of the swarming season in the zones indicated by the numbers in Figure 1*a*. Figure 3 was derived from replies of fishermen to the

question, "In what month(s) do you *usually* observe the euphausiid swarming in your favorite fishing grounds?" The three degrees of swarming intensity of euphausiids were fixed as follows: 1–3 affirmative response(s) from a certain zone in a given month were expressed by a white area, 4–6 affirmative responses by a shaded area, and more than 7 by a black area. Actually, each month expressed by a black area represents more than 15 affirmative responses.

Figure 3 also indicates that the major swarming regions in the coastal areas of the Sea of Japan are around Sadogashima (zone 8), in Wakasawan and vicinity (zones 15 and 16), off Sanin district including Oki (zones 18–21), and on the east side of the Tsushima Gunto (zone 24).

There seems to be a tendency for swarming to take place earlier in the year in the southern part of the Sea of Japan. Thus, in the north of Kyushu (zones 23–25), the most intensive swarming is observed in February and March; in the Wakasawan and Sanin districts (zones 15–21), the most notable swarming season is in March and April (also in May in some zones); and in the area surrounding Sadogashima (zone 8), the euphausiids aggregate most actively in April through June. According to the fishermen's information, the swarming season in each zone changes from year to year, as in the Kinkazan waters. The beginning, peak, and terminating times of the swarming are different from year to year. The swarming season along the coasts of the Sea of Japan occurs between January and June.

Seasonal Change of Water Temperature

Figure 4 shows the mean surface temperature and salinity cycles throughout a year at three representatives coastal points in the Sea of Japan. All temperature records for a given month, taken over a period of 26 years, were averaged. The same was done with salinity determinations.

Upon comparing Figure 4 with Figure 3, it may be seen that the occurrence of swarming is closely associated with colder water temperatures. Swarming starts at a slightly higher temperature than the local minimum, continues with increasing temperature, and then terminates as the temperature exceeds 16°C. The
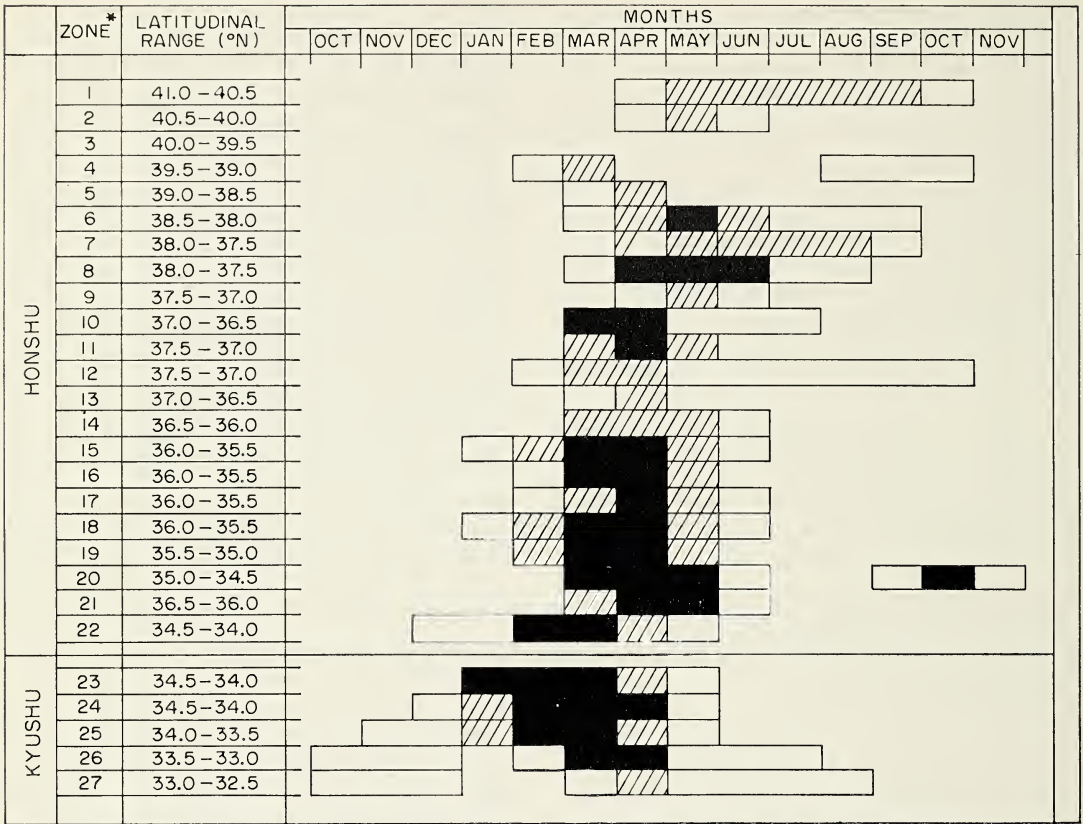
Fig. 3. Swarming season of *Euphausia pacifica* in the coastal areas of the Sea of Japan (see text). Zones are shown in Figure 1*a*.

temperature during the swarming season ranges between 7° and 16°C.

Figure 5*a* shows the average change of surface water temperature during the first six months at Enoshima, a tiny island located in the middle of the fishing ground for euphausiids around Kinkazan (Fig. 1*b*). Daily hydrometerological observations have been made at this island since 1910, with an interruption during the period from 1945 to 1953. In this Pacific coastal region, swarming starts with the minimum surface water temperature (in February and March), continues as the temperature rises, and ends when it reaches about 12°C, thus demonstrating again a relationship between swarming and low temperature.

The vertical distribution of temperature and its annual change was also examined for the Kinkazan waters. Figure 6 shows the mean annual changes of temperature profiles down to 200 m at two points 10 miles off Ozaki (*a*)

and Shioyazaki (*b*), respectively. It was not possible to learn the results of long-term oceanographic observations carried out at a definite station adequately close to Kinkazan, which would have been an ideal station. Therefore these two stations were substituted. Monthly observations have been made along the west-east lines, including the above two stations as the nearest ones to the coast, for 20 years off Ozaki and for 24 years off Shioyazaki. Figure 6 shows that sea water is completely mixed from the top down to a depth of 200 m, and that a low temperature prevails during the months corresponding to the swarming season of euphausiids.

It seems probable that the water temperature profile in the euphausiid fishing ground near Kinkazan is more nearly similar to that off Ozaki than to that off Shioyazaki, which is located in the south where the sea conditions are more directly influenced by the warm
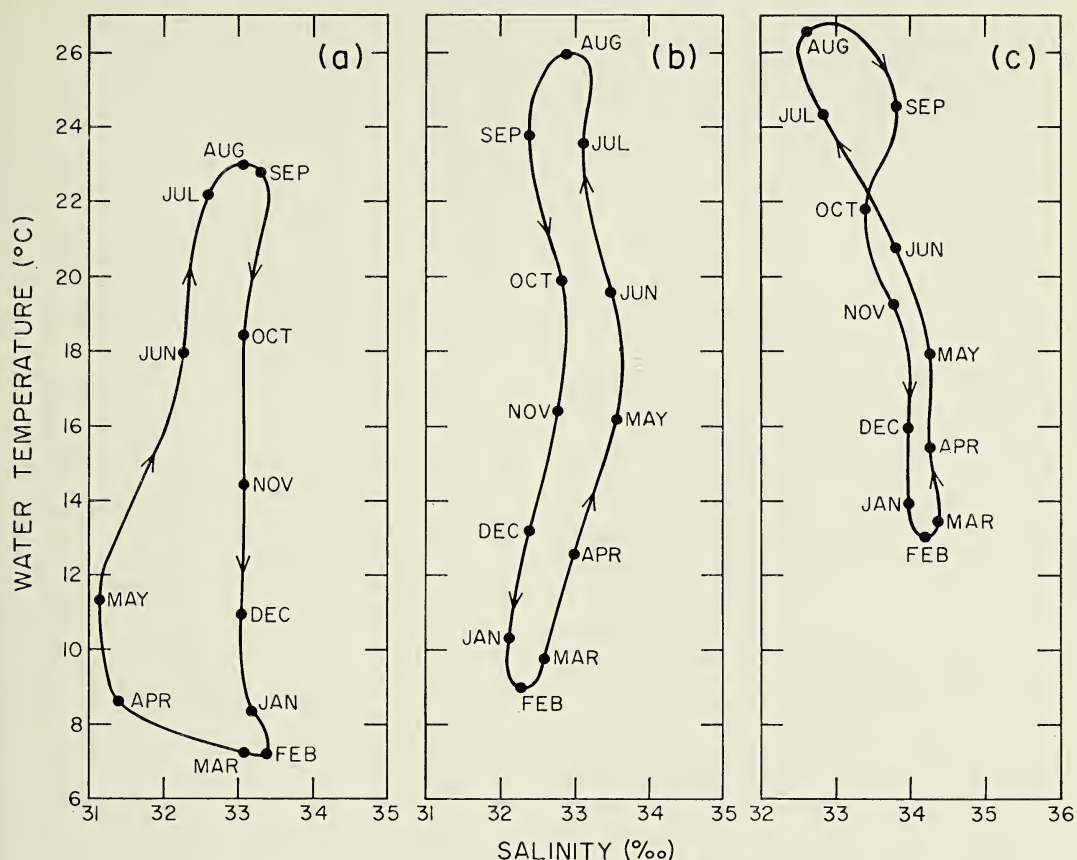
FIG. 4. Annual changes of surface water temperature and salinity at Nyudozaki (*a*), Kyogasaki (*b*), and Okinoshima (*c*). Locations are shown in Figure 1*a*. Measurements were made from 1915 to 1950 with interruptions in some years.

Kuroshio. Such a condition of low and uniform temperature as prevails from the surface down to 200 m in the vicinity of Kinkazan provides no temperature barriers to euphausiids that may be dwelling in the depths (Boden and Kampa, 1958). In other words, euphausiids, during their vertical migration, do not encounter the temperature difference between day and night levels that has been discussed by H. B. Moore (1952).

Annual Variations in Swarming

The statistics for annual yields of euphausiids recorded at the Onagawa fish market (Table 2) indicate remarkable annual changes in euphausiid abundance in the vicinity of Kinkazan. Each value in Table 2 can be interpreted as an index of the standing crop of swarming euphausiids in each swarming sea-

son, because there were no notable changes in fishing effort (i.e., the number of fishing boats) throughout these seven years, and almost all euphausiids fished in the area were landed at the Onagawa fish market.

Similarly, in the nearshore waters of the Sea of Japan, it was also observed that the extent of swarming fluctuates widely from year to year. Although profuse swarming occurred during the period from 1943 through 1949 (Uda, 1952), it has been observed only rarely since 1953. The relative abundance of euphausiid swarming during the period 1945–1956 in the nearshore waters of the Sea of Japan is shown in Figure 7. Each symbol represents an answer from an individual fisherman. Figure 7 illustrates that intensive swarming in the Sea of Japan took place until 1953 but ceased thereafter. Although no numerical data

TABLE 2

ANNUAL YIELDS OF *Euphausia pacifica* FROM THE KINKAZAN AREA*

YEAR	YIELD (TONS)
1953	431.8
1954	0.0
1955	887.1
1956	1,029.2
1957	274.0
1958	404.1
1959	1,419.1

* From the statistics of the Onagawa fish market.

are available, the information at hand indicates that the disappearance of swarms from near-shore waters continued at least until 1958.

In order to relate the annual change in the euphausiid swarming to the surface water temperature, examination of water temperatures during the first six months of the year at Enoshima (Fig. 5a) are plotted in Figures 5b (1954) to 5g (1959) with 10-day intervals. Each point represents the mean values of 10 daily measurements.

Upon relating Figure 5 to Table 2, it is quite obvious that the temperature was abnormally higher than the mean throughout the winter and spring of 1954, when absolutely no euphausiids were caught. On the other hand, in 1956 and 1959, when more than 1,000 tons of euphausiids were captured, the temperature was a little lower than the mean in February and March 1956, and it was a little higher than, but close to, the mean in April and May 1959. Euphausiids were fished mainly in the early spring of 1956, while they were caught more abundantly late in the spring of 1959 than earlier (Fig. 2).

The peculiarity of the water temperature in the winter and spring months of 1954 also can be learned from Figure 8. Figure 8 is based on the monthly observations at the station 10 miles off Tsubakishima (Fig. 1a), which is located closer to Kinkazan than is Ozaki. Figure 8a shows the water temperature profile down to a depth of 200 m during the period from November 1953 to November 1954. Figure 8b shows the temperature profile at the same station for the following year. It is obvious that a remarkable temperature gradient was present during the winter and spring months of 1954, when no euphausiids were
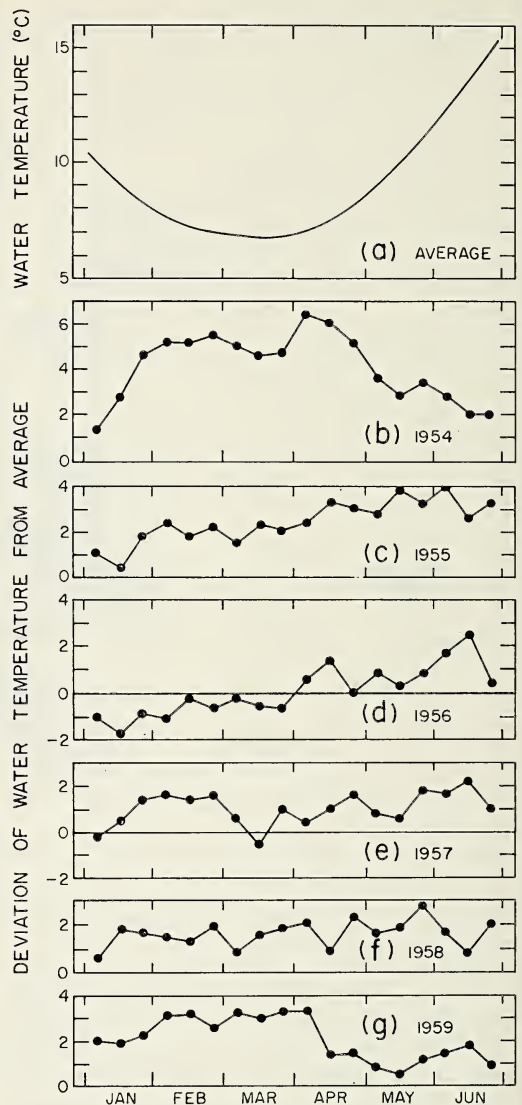
FIG. 5. Surface water temperatures at Enoshima. (a), Average temperatures for 1910–1944 and 1953–1959; (b)–(g), deviations from the mean for 1954–1959.

captured. Considerable warm water occupied the surface layers in the spring of 1954, especially in April, which corresponds to the middle of the swarming season in the Kinkazan waters. The temperature profile for the next year (Fig. 8b) shows normal seasonal change in the area, as is indicated by the temperature profiles at the stations off Ozaki and Shioyazaki (Fig. 6).

The records of water temperatures observed
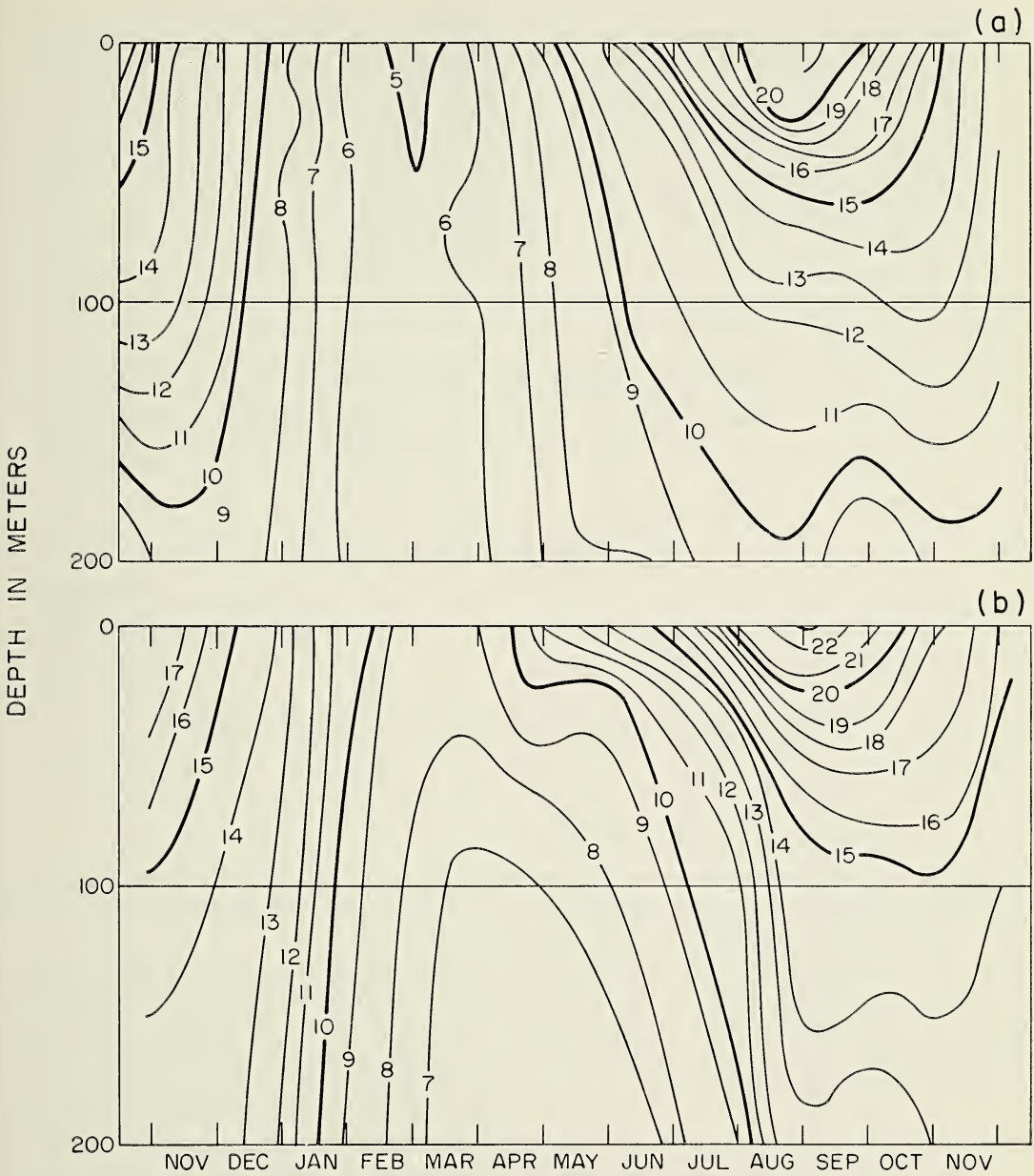
Fig. 6. Average annual changes of water temperature profile 10 miles off (*a*) Ozaki during 1919–1939, and (*b*) Shioyazaki during 1914–1939. Locations are shown in Figure 1*a*.

at Kyogasaki were the only data available for relating temperature to the long-term change in swarming in the Sea of Japan shown in Figure 7. The monthly mean values of water temperatures in a given month from 1943 to 1957 are plotted in Figure 9. It appears that all water temperatures in March, from 1943 to 1952, were lower than the accumulated av- erage value calculated over the years beginning with 1915 (dashed lines in Fig. 9). March is the month when swarming takes place exten- sively in the Wakasawan area. Also, the least squares regressions (solid lines in Fig. 9) ob- tained from values during these 14 years sug- gest an explanation for the disappearance of euphausiids from the neritic areas. All regres-
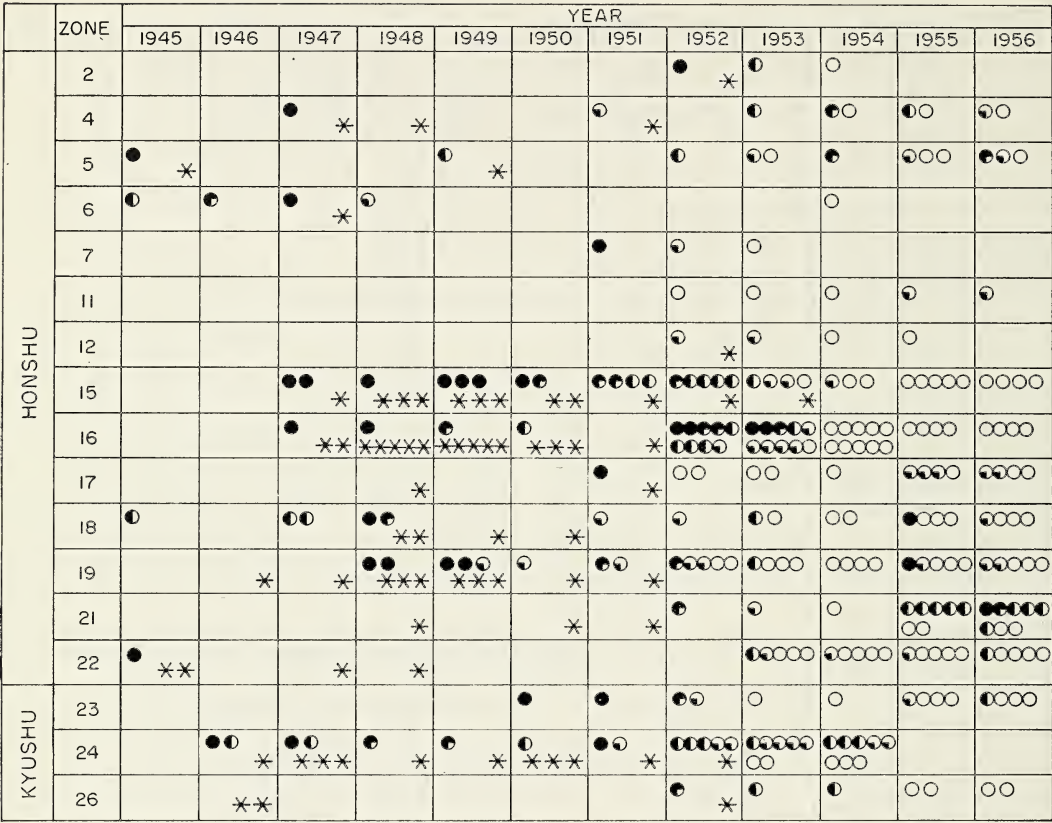
FIG. 7. Fluctuation in relative abundance of *Euphausia pacifica* swarming at the surface in the coastal areas of the Sea of Japan. (1) a few, (2) less than usual, (3) usual, (4) more abundant than usual, (5) much more abundant than usual, (6) extraordinarily abundant.

sions have a positive slope, which means that successive years tended to be warmer during this period, and this tendency is greatest in March and April (Fig. 9*b* and *c*) when the most extensive swarmings take place.

Predators

It was learned from fishermen that there is a close relationship between the abundance of euphausiids at the sea surface and fishes in the swarming areas of euphausiids. Various previous workers—Smith (1879), Lebour (1924), MacDonald (1927), Hjord and Ruud (1929), Sheard (1953), Zelickman (1961), and Marr (1962) among others—also reported the euphausiid swarms accompanied by predators such as fishes, whales, and birds. In order to

take this relationship into account, an investigation was made on representative predators.

Figure 10 shows the change in annual yield of Japanese mackerel, *Scomber japonicus*, from the Wakasawan area. This was obtained from the statistics of the Ministry of Agriculture and Forestry. Spring mackerel fishing in the area usually is carried out during the period approximately corresponding to the swarming season of euphausiids, and examination of stomach contents of mackerel has shown that the mackerel is predatory on euphausiids. A conspicuous increase in the yield from 1945 to 1946 (Fig. 10) probably was caused by restoration of the local fishing fleet from the wartime decline, i.e., the increase of fishing effort. In 1949, when an extraordinary abundance of
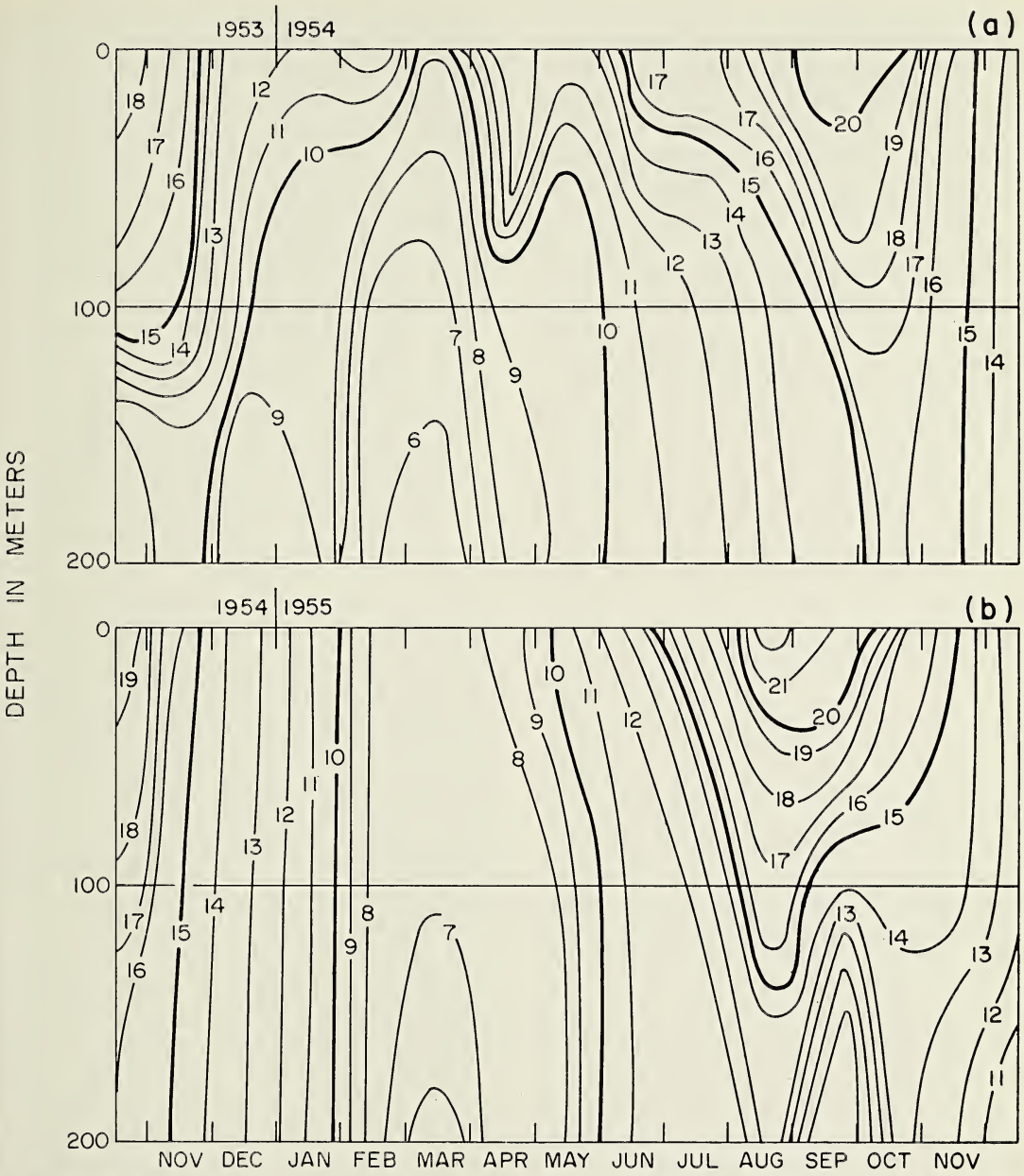
FIG. 8. Water temperature 10 miles off Tsubakishima. Location shown in Figure 1*a*. (*a*), Fall 1953 to fall 1954; (*b*), fall 1954 to fall 1955.

mackerel was fished, abnormally conspicuous swarming of euphausiids was observed in this area (Fig. 7). Rapid decrease in mackerel yield occurring in 1952 and thereafter may be related to the disappearance of the spring swarms of euphausiids from the coastal area after that year.

Table 3 shows the change in annual yield of sand eel, *Ammodytes personatus,* from the Kinkazan waters. In general, the fishing season of sand eel in this area starts in January and terminates by the end of July, and they are taken from almost the same area as the euphausiid fishing ground shown in Figure 1*b*.
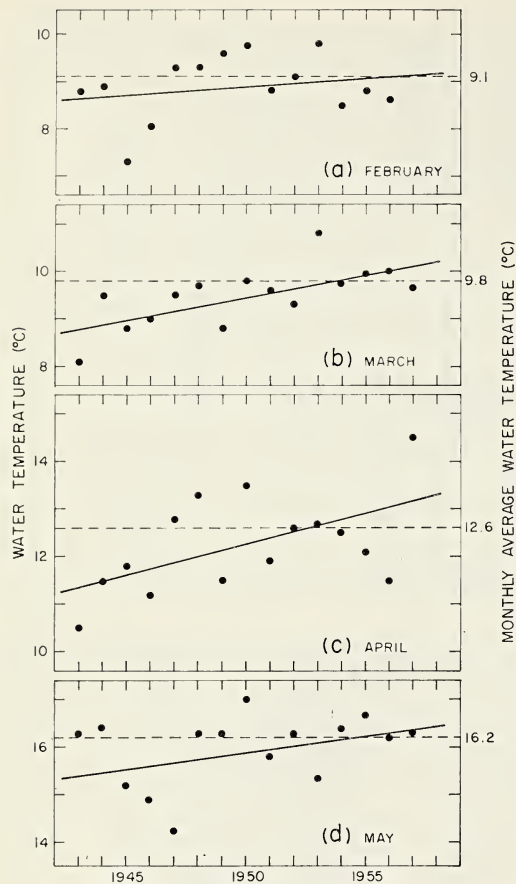
FIG. 9. Monthly mean temperature in each of four spring months from 1943 through 1957 at Kyogasaki. *Dashed lines* show mean temperatures, 1915–1957; *solid lines* show least squares regressions for 1943–1957.

Comparing Table 3 with Table 2, it is obvious that annual yields of both euphausiids and sand eel from the area fluctuate in parallel.

In addition to the sand eel, the sea gull, *Larus crassirostris,* and a small blackish bird, *Cerorhinca monocerata,* can be considered predators on euphausiids in the Kinkazan waters. According to local fishermen, *C. monocerata* can dive into the deep, and it probably attacks submerged euphausiids from the bottom and drives them up to the surface.

DISCUSSION

It has been clearly demonstrated here that the swarming of *Euphausia pacifica* in the nearshore waters of Japan is closely related to
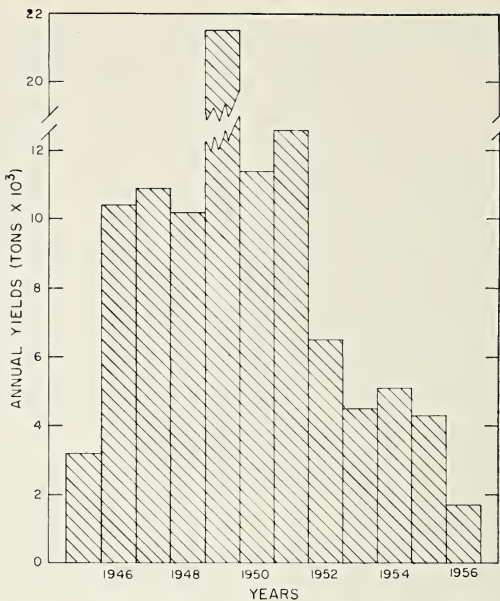
FIG. 10. Annual yield of Japanese mackerel, *Scomber japonicus,* from the Wakasawan area.

cold water temperatures. This may be expected, since the species is a boreal form, occurring commonly north of the subarctic convergence, as shown by Banner (1949), Boden et al. (1955), Nemoto (1957), Brinton (1962a), and Ponomareva (1963). The habitat is crescent in shape, covering the northern part of the North Pacific. *E. pacifica* occurs in the cold water lying under the upper strata in the Sea of Japan (Komaki and Matsue, 1958).

Inasmuch as the branches of the warm Kuroshio wash the Japanese coasts, *E. pacifica* may be excluded from the coastal areas except during the coldest season, while it is more commonly concentrated in the nearshore and inshore waters of the eastern North Pacific (Banner, 1949; Boden et al., 1955; Brinton, 1962a, b; Banse and Semon, 1963; Regan, 1963). Except during its swarming season,

TABLE 3

ANNUAL YIELD OF SAND EEL, *Ammodytes personatus,* FROM THE KINKAZAN AREA*

YEAR	YIELD (TONS)
1953	741.7
1954	349.6
1955	580.8
1956	4,029.1

* From the statistics of the Onagawa fish market.

E. pacifica is seldom found in the stomachs of various fishes caught on the continental shelves around Japan. Therefore, the approach of the offshore populations of *E. pacifica* into near-shore waters must be the first step of swarming in the coastal area around Japan. It may be considered as a seasonal expansion of their distribution to the coastal areas, inasmuch as Beklemishev and Semina (1956) and Semina (1958) demonstrated that the seasonal change of zoo- and phytogeographical boundaries accompanied the seasonal shift of the convergence between Kuroshio and Oyashio.

The size of the approaching offshore populations may be strongly influenced by temperature conditions from year to year. Uda (1964) illustrated and discussed the meanderings of the Kuroshio. Masuzawa (1960) discussed the annual variation of the Kuroshio axis, and showed that the north-south swing of the axis around the point of 36°N, 144°E was much greater than that of the other portions, and also that there is a possibility that the isolation of the water bodies may take place at the top of the conspicuous current axis curvature. The point mentioned above is located in the southeast off Kinkazan, and therefore it is quite possible that an isolated warm water mass from the top of the northward curvature of the Kuroshio approaches the coastal region around Kinkazan in some cases. The extraordinarily high temperature observed in the winter and spring months of 1954 possibly was caused by such an approach of the isolated water mass, although Masuzawa's data of 1954 through 1959 showed that the northernmost meandering of the current axis occurred in 1955 and not in 1954.

Miyata and Shimomura (1959) and Miyata (1960) classified several cold water masses in the offshore areas of the Sea of Japan and discussed their location and transference. Uda (1952, 1958) discussed the variation of the conditions in this sea, describing the change of the position of the polar front from year to year. It cannot be doubted that the offshore cold water masses come close to the Honshu coasts in winter and spring when the monsoon blowing from Siberia prevails.

Actually, the cold water masses defined by the above workers are located off the zones where the swarming of euphausiids takes place most actively, e.g., around Sadogashima (zone 8), in the Wakasawan area (zones 15 and 16), and around Oki (zone 21) (Fig. 1*a*). In winter and spring these cold water masses may protrude against the coastal areas in the manner of a tongue. The warm water of the Tsushima current is very shallow because of the shallowness (about 100 m) of the Tsushima Kaikyo. Accordingly, it is likely that the originally warm Tsushima current water will be mixed with cold water masses through relatively simple processes.

The stronger the approach of offshore cold water masses to the coast and the stronger the mixing in the coastal areas, the more profuse will be the swarmings of euphausiids along the coasts on the Sea of Japan. As a matter of fact, Uda (1958) showed that the polar front came very close to the Honshu coast during the period from 1946 to 1949, while it was away from the coast after 1952. It appears that such approach and recession of the polar front corresponds in time to the change in swarming (Fig. 7).

Thus, low temperature induces the coastward approach of the offshore stocks of *E. pacifica,* and it must be one of the indispensable conditions for surface swarming in Japanese nearshore areas. However, it would be premature to conclude that it is the only sufficient condition. One is still unable to explain why euphausiids do not swarm in early and middle winter months when the temperature is as low as it is in spring and vertical mixing is actively taking place, and why they come to the surface in the daytime when the light intensity may be harmful to them.

There have been several different opinions as to the cause of the daytime surface-swarming of euphausiids: (a) Predators may drive euphausiids to the surface, as previously mentioned. (b) Euphausiids come to the surface to search for food in the upper strata where phytoplankton is abundant (Paulsen, 1909; Manteufel, 1938, 1941). (c) Current conditions may accumulate euphausiids, or stimulate them to swarm at the surface (Fish and Johnson, 1937; Einarsson, 1945; Peters, 1955). (d) Some internal demands related to maturation or reproduction may drive euphausiids

to the sea surface (Sheard, 1953; Ponomareva, 1959, 1963; Zelickman, 1961). Although these theories are still controversial, the last can probably be applied to the swarming of *E. pacifica* in Japanese nearshore waters.

The author observed that more than 50% of the females in a few swarms in the Sea of Japan had spermatophores in the thelycum. No specimens from the Kinkazan area were carrying spermatophores. However, the females were full-grown and the degree of maturation of the ovaries corresponded to the stage 3 defined by Ruud (1932) or to the stage 5 or 6 established by Bargmann (1945) for *Euphausia superba*. As is shown in Figure 2, offshore populations of *E. pacifica* seem to come close to the coast around Kinkazan with a pulselike rhythm. This may suggest that the population of *E. pacifica* can be divided into several stocks in accordance with the phase of maturation, and that, as stocks reach a certain degree of maturity, they approach the coast in succession. The tendency for swarming to occur earlier in the southern part of the Sea of Japan than in the northern part, as shown in Figure 3, may be understood in relation to the geographical difference between the maturing or reproduction phases of euphausiids and to seasonal differences in temperature of the two areas.

Kun's opinion (1955) on the daytime ascent of *Calanus tonsus,* which may be related to a biochemical process (e.g., transformation of vegetable carotenoids into vitamin A by ultraviolet radiation) may be applied to the swarming of euphausiids. During certain periods of their maturing or reproductive process, euphausiids might need rather strong daylight, regardless of the usual daytime level of their vertical distribution. As listed in Table 1, nearly all species whose swarming has been reported hitherto are cold water forms. This suggests that their physiology should be analyzed, with the objective of solving the mechanism of this peculiar behavior of euphausiids.

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The Ecology of Pelagic Amphipoda, II

Observations on the Reproductive Cycles of Several Pelagic Amphipods from the Waters off Southern California

Gary J. Brusca[1]

The purpose of this study was to utilize mid-water samples from off the coast of southern California to determine the general patterns of the reproductive cycles of the local pelagic Amphipoda. All of the materials analyzed during this project were collected in the area of the Outer Santa Barbara Passage at approximately 33°20′N, 118°40′W. All samples were collected with an Issacs-Kidd Midwater Trawl (Issacs and Kidd, 1953) from the R/V "Velero IV" of the Allan Hancock Foundation, University of Southern California. Partial support for this work was furnished by National Science Foundation Grants (G10691 and G23467).

Complete information on the reproductive cycles of amphipods is scarce and, in the case of pelagic species, difficult to obtain. Some data can be gained from various expedition reports in which the presence of ova and young in the brood pouches is recorded. Some of these past records are mentioned in this paper.

METHODS AND MATERIALS

Samples were taken at various depths and at different times of the day and night from the summer of 1962 through the spring of 1963 using a 10 × 10-ft Issacs-Kidd Midwater Trawl. A few samples were used from later in 1963 for qualitative confirmation of the data gathered earlier. Species accounts and analyses of vertical distributions and migrations are presented by Brusca (1967).

For comparative information on fluctuations in population densities throughout the year, counts made from pint aliquots were converted to the number of individuals captured per hour trawling time. Such values are only approximate and do not account for the suspected gregarious nature of these pelagic amphipods, but they probably do reflect the general trends in the population size. Complete raw data are on file with the author.

OBSERVATIONS

Presented in this section are only those data which specifically pertain to the reproductive cycles of these animals. For a more detailed species account and reference lists see Brusca (1967).

Suborder GAMMARIDEA

Family EUSIRIDAE

Rhachotropis natator (Holmes)

A total of 77 specimens was taken from pint aliquots. None of these individuals was noted to be carrying ova or young in the brood pouches, but there was some variation in the size range and in the density of the population. Table 1 illustrates these changes.

Since a rise in population density accompanied an extension of the lower limit of the size range during the winter months, this time probably represents the entrance of young into the adult or "catchable" population. The data

TABLE 1

SEASONAL CHANGES IN SIZE RANGE (SR), AND AVERAGE NUMBER PER TRAWL HOUR (n/th) BASED ON POSITIVE SAMPLES FOR *Rhachotropis natator*

SEASON	SR (mm)		n/th
Summer	20	(1 spec)	4
Fall	13–17		22
Winter	9–16		32
Spring	9–17		24

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are too scant, however, to draw any definite conclusions.

Family LYSIANASSIDAE

Paracallisoma coecus (Holmes)

During this study 56 specimens were recovered from pint aliquots. The presence of ovigerous females was noted in October and November and a few were carrying young in May. Seasonal variations in number and size offer no conclusive data due to the small quantity of individuals collected.

Cyphocaris anonyx Boeck

A total of 115 individuals was collected from pint aliquots. Ovigerous females were noted during the months of May, June, July, and August, indicating that this season is a time of high reproductive activity. No females were found which were carrying young. As shown in Table 2, there was an extension of the lower limit of the size range during the summer months and an increase in population density, probably indicating the entrance of young into the mature population. The drop in mean size in the fall may reflect the death of the older portion of the population.

Cyphocaris richardi Chevreux

A total of 193 specimens was sorted from pint aliquots. Table 3 illustrates the pertinent reproductive information.

As can be seen, the greatest production of eggs occurred during the fall months, and young were present in the brood pouches only in the winter. Males were most abundant at the times of high ova production. It appears that embryonic development took place through-

out the winter months, with the release of young completed by early spring.

There was a slight drop in mean size and in the lower limit of the size range in the spring, followed by a more drastic decrease in these measurements during the summer. These periods indicate the time of the entrance of young into the adult population.

Suborder HYPERIIDEA

Family PLATYSCELIDAE

Platyscelus serratulus Stebbing

Only 8 specimens of this species were taken, all of which were females. Although Hurley (1956) collected P. serratulus from southern California waters during the months of January and February, the individuals captured during this present study were taken in September and November. Ovigerous females were noted in November. Sizes ranged from 3 to 7 mm with a mean of 5.1 mm for the 8 specimens collected.

Family PRONOIDEA

Eupronoe minuta Claus

In all, 322 individuals were collected from pint aliquots. From the data presented in Table 4 it can be seen that some of the reproductive activity of E. minuta is not clear, in that the greatest production of ova occurred at the same time as the highest incidence of young in the brood pouches. Apparently young were released from the females early in the fall. This release is indicated by a drop in the percentage of females carrying young, a drop in mean size, and an extension of the lower limit of the size range. Males were present only during the fall months, suggesting that that was the period of fertilization.

Family PHROSINIDAE

Primno macropa Guerin

A total of 315 individuals was taken from pint aliquots. The pertinent reproductive data are recorded in Table 5.

Maximum production of eggs occurred in the

TABLE 2

SEASONAL VARIATION IN MEAN SIZE (MS), SIZE
RANGE (SR), AND AVERAGE NUMBER PER
TRAWL HOUR (n/th) FOR
Cyphocaris anonyx

SEASON	MS (mm)	SR (mm)	n/th
Summer	11.5	4–14	37
Fall	8	6–12	4
Winter	13.5	5–15	13
Spring	10	7.5–13.5	30

TABLE 3

SEASONAL VARIATIONS IN THE PERCENTAGES OF MATURE FEMALES CARRYING OVA (O), CARRYING
YOUNG (Y), MEAN SIZE (MS), SIZE RANGE (SR), FEMALE/MALE RATIO (f/m), AND THE
AVERAGE NUMBER PER TRAWL HOUR (n/th) BASED ON POSITIVE SAMPLES
FOR *Cyphocaris richardi*

SEASON	O	Y	MS(mm)	SR(mm)	f/m	n/th
Summer	10%	0%	20	11–29	1.5/1	33
Fall	43%	0%	22	17–28	0.7/1	56
Winter	10%	13%	26	18–33	1/1	51
Spring	14%	0%	24	15–30	1.6/1	48

TABLE 4

SEASONAL VARIATION IN THE PERCENTAGES OF MATURE FEMALES CARRYING OVA (O) AND
YOUNG (Y), MEAN SIZE (MS), AND SIZE RANGE (SR), AND AVERAGE NUMBER PER TRAWL
HOUR (n/th) FOR *Eupronoe minuta*

SEASON	O	Y	MS(mm)	SR(mm)	n/th
Summer	35%	15%	6	4.2–7.8	4
Fall	26%	0%	5.5	3–7.5	26
Winter	10%	0%	5.5	3.5–7.5	8
Spring	25%	15%	5.7	5–7	5

TABLE 5

SEASONAL VARIATION IN THE PERCENTAGES OF MATURE FEMALES CARRYING OVA (O), AND
YOUNG (Y), MEAN SIZE OF FEMALES (MSf), AND MALES (MSm), SIZE RANGE OF
FEMALES (SRf), AND MALES (SRm), AND AVERAGE NUMBER PER TRAWL
HOUR (n/th) FOR *Primno macropa*

SEASON	O	Y	MSf	MSm	SRf(mm)	SRm(mm)	n/th
Summer	50%	5%	7	5	4–12	4–9	5
Fall	50%	3%	8.5	4.5	4–12	4–5	26
Winter	33%	0%	7	none	5–13	none	4
Spring	27%	25%	12	none	6–14	none	4

summer and fall months, with a high percentage of the females carrying young by spring. Males were captured only during times of highest ova production. The young were released into the adult population during the summer, as indicated by a drop in mean size, an extension of the lower limit of the size range, and an increase in the average number per trawl hour by the fall months.

Family CYSTISOMIDAE

Cystisoma fabricii Stebbing

Only 31 specimens were collected. Ovigerous females were noted in October and December, and some were carrying young during January and August. There was an increase in the number of males collected at times of ova production. Because of the paucity of specimens no definite conclusions can be drawn.

Cystisoma pellucidum (Suhn)

Only 4 individuals were collected during the entire study period, including a single ovigerous female in July (64 mm). Other specimens were taken in August (male, 70 mm), January (male, 116 mm), and May (damaged, 70 mm).

Family OXYCEPHALIDAE

Calamorhynchus pellucidus Streets

A single male specimen (19 mm) was collected during September. Fage (1960) gave an account of the known reproductive biology of

TABLE 7

SEASONAL VARIATION IN THE PERCENTAGES OF MATURE FEMALES CARRYING OVA (O) AND YOUNG
(Y), MEAN SIZE OF FEMALES (MSf) AND MALES (MSm), SIZE RANGE OF FEMALES (SRf)
AND MALES (SRm), AND THE FEMALE/MALE RATIO (f/m) OF *Hyperia galba*

SEASON	O	Y	MSf(mm)	MSm(mm)	SRf(mm)	SRm(mm)	f/m
Summer	0%	45%	9	12	8–12.5	11–13	4.5/1
Fall	10%	17%	9	11.5	6–19.5	9–15	4.6/1
Winter	50%	18%	10.5	10.5	7.5–12.5	6–15	1.5/1
Spring	98%	0%	9	11.5	8.5–10	8.5–17	1.5/1

tive information. Egg production was highest in the summer months, and the highest incidence of young in the brood pouches was in the spring. The abundance of males does not appear to correlate with the presence of ova. Young were released from the parents by summer, but their entrance into the mature population was not reflected in the size data until fall, at which time there was an extension of the lower limit of the size ranges for both males and females. This suggestion is also supported by an increase in population density from an average of 3 individuals per trawl hour in the summer to 10 per trawl hour during the fall months. There appears to be about a three-months' lag between the release of young from the brood pouches and their entrance into the catchable population. The whereabouts of the newborn amphipods is unknown. Analyses of local plankton samples taken during the suspected time of release offered no positive information.

Family VIBILIIDAE

Vibilia armata Bovallius

A total of 2,742 individuals was sorted from pint aliquots. Some of the reproductive data

for this species are difficult to interpret. Stephensen (1918) reported on collections from the Mediterranean in which he found breeding females in January and February and from June through September and young at all times of the year. In this present study no ovigerous females were noted during the winter and only a low percentage was recorded for the rest of the year (Table 8). The presence of young in the brood pouches suggests that the release from the parents took place in the late spring and early summer, at which time an extension of the lower limit of the size range and a drop in mean size were noted. The population density, however, did not show a significant increase until early fall.

Vibilia viatrix Bovallius

In all 658 individuals were recorded from the sorting of pint aliquots. Stephensen (1918) reported specimens of *V. viatrix* in breeding condition during March and October in the North Atlantic. The information gathered in this present study is given in Table 9.

Ovigerous females were most abundant in the fall and a high percentage was carrying young by winter. Apparently juveniles were released from the brood pouches during the

TABLE 8

SEASONAL VARIATION IN THE PERCENTAGES OF MATURE INDIVIDUALS CARRYING OVA (O) AND
YOUNG (Y), MEAN SIZE (MS), SIZE RANGE (SR), AND AVERAGE NUMBER PER TRAWL
HOUR (n/th) FOR *Vibilia armata*

SEASON	O	Y	MS(mm)	SR(mm)	n/th
Summer	3%	10%	6.5	3–10	14
Fall	8%	35%	7.5	6–10	251
Winter	0%	45%	7	6–9	71
Spring	8%	51%	8.5	6–10	30

TABLE 9

SEASONAL VARIATION IN THE PERCENTAGES OF MATURE INDIVIDUALS CARRYING OVA (O) AND
YOUNG (Y), MEAN SIZE (MS) AND SIZE RANGE (SR), AND AVERAGE NUMBER PER TRAWL
HOUR (n/th) FOR *Vibilia viatrix*

SEASON	O	Y	MS (mm)	SR (mm)	n/th
Summer	12%	25%	9	4–15.5	38
Fall	20%	40%	9	7–12	8
Winter	9%	60%	10.5	7–14	5
Spring	3%	21%	11.5	8.5–15	3

spring and summer months, as is shown by a drop in mean size and an extension of the lower limit of the size range along with an increase in the average number per trawl hour. All of these indications became obvious during the summer.

Family PHRONIMIDAE

Phronima sedentaria (Forskål)

A total of 575 individuals was sorted from pint aliquots. Previously reported reproductive data on *P. sedentaria* were reviewed by K. H. Barnard (1932), who indicated that, in the more northern regions of its distribution, this species has its highest period of reproductive activity during the summer and fall months. Table 10 gives the breeding information gathered in this present study.

The peak of egg production occurred in the summer. Since the developing young of this species are carried for some time on the inner walls of the salp "barrels" in which *P. sedentaria* is known to live, and only a few of these "barrels" were collected, probably the percentages of females with young are inaccurate.

Because of the confusion regarding the release of young from the parents (or from the barrels), it is difficult to analyze the size variations as related to breeding season. In addition to this problem, one can see from Table 10 that the extensions of the lower limits of the size range for males and females do not coincide. In spite of these difficulties, however, males were most prevalent during the times of high egg production and the other data do indicate greatest reproductive activity during the summer and fall months, concurring with Barnard's 1932 report.

Family PARAPHRONIMIDAE

Paraphronima gracilus Claus

A total of 472 specimens was collected from pint aliquots. Hurley (1956) reported a single female with young in the brood pouches during August. His work was conducted in the local southern California area near the collection sites of this present study.

As indicated in Table 11, the highest percentages of ovigerous females were noted in the fall and females carrying young were most

TABLE 10

SEASONAL VARIATION IN THE PERCENTAGES OF MATURE FEMALES CARRYING OVA (O) AND YOUNG
(Y), THE MEAN SIZE OF FEMALES (MSf) AND MALES (MSm), SIZE RANGE OF FEMALES (SRf) AND
MALES (SRm), THE FEMALE/MALE RATIO (f/m), AND THE AVERAGE NUMBER PER TRAWL
HOUR (n/th) FOR *Phronima sedentaria*

SEASON	O	Y	MSf (mm)	MSm (mm)	SRf (mm)	SRm (mm)	f/m	n/th
Summer	53%	20%	25	16	11–35	11–17	2.4/1	20
Fall	20%	3%	22	14	14–33	9–18.5	2.2/1	15
Winter	7%	22%	27	13	13–35	11–15	10/1	8
Spring	25%	19%	28	none	18–37	none	no males	3

TABLE 11

Seasonal Variation in the Percentages of Mature Females Carrying Ova (O) and Young (Y), Mean Size of Females (MSf) and Males (MSm), Size Range of Females (SRf) and Males (SRm), and the Average Number per Trawl Hour (n/th) for *Paraphronima gracilus*

SEASON	O	Y	MSf(mm)	MSm(mm)	SRf(mm)	SRm(mm)	n/th
Summer	8%	50%	13.5	10.5	9–16.5	10–14	8
Fall	43%	47%	10	10.5	9.5–13	10–11	33
Winter	24%	55%	11	10.5	10–12	10–11	18
Spring	2%	75%	11	11	10–12	10–12	20

TABLE 12

Seasonal Variation in the Percentages of Mature Females Carrying Ova (O) and Young (Y), Mean Size of Females (MSf) and Males (MSm), Size Range of Females (SRf) and Males (SRm), and the Average Number per Trawl Hour (n/th) for *Paraphronima crassipes*

SEASON	O	Y	MSf(mm)	MSm(mm)	SRf(mm)	SRm(mm)	n/th
Summer	7%	50%	20	16.5	14–28	13.5–23	16
Fall	49%	49%	19	18.5	13–26.5	14–23	40
Winter	24%	56%	22	20	20–28	18–22	52
Spring	2%	75%	24	18.5	13.5–31	13–24	41

abundant in the summer. The female/male ratio was relatively low at the suggested time of ova production (2/1), and there was an increase in the average number per trawl hour from 8 per trawl hour in the summer to 33 per trawl hour in the fall, indicating the release of young into the mature population. There was also a drop in the mean size of the female population during the fall, but other size data offer no correlations.

Paraphronima crassipes Claus

A total of 922 individuals were recovered from pint aliquots. Hurley (1956) reported specimens collected in local waters during July and August to be carrying ova or young in their brood pouches. Table 12 gives the reproductive information regarding *P. crassipes* gathered in this present study.

The highest percentage of females with ova was noted in the fall, followed by a high incidence of young in the brood pouches in the winter and spring. Apparently young were released from most of the females in the summer and fall, during which time there was a drop in mean size and, by fall, an increase in the population density. The ratio of females/males was lowest during the fall (1/1), corresponding with the production of eggs.

CONCLUSIONS

During this study certain general trends were noted regarding the reproductive activity of the total amphipod population. As illustrated in Table 13, the highest production of ova occurred during the summer and fall months, with development of young continuing throughout the following spring and summer. Most species released their young into the adult population by early fall, as indicated by the percentages listed in Table 13 along with the increase in the total amphipod population density.

It can be seen that, although the above mentioned trends are observed, precise analyses of the activities of individual species are complex and difficult to make. A sampling program de-

TABLE 13

Seasonal Variation in the Percentages of Mature Females with Ova (O) and Young (Y) in the Brood Pouches, and the Number per Trawl Hour (n/th) for the Total Amphipod Population

SEASON	O	Y	n/th
Summer	24%	40%	49
Fall	20%	32%	135
Winter	10%	35%	50
Spring	14%	43%	40

signed specifically to obtain large numbers of individuals throughout the year is needed in order to eliminate density errors due to vertical migrations and gregarious activity. The fact that amphipods brood their young makes the group an ideal one for embryological studies if enough material can be obtained. The development and ecology of newborn amphipods could provide excellent problems for future research.

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The Zoeal Stages and Glaucothoe of the Tropical Eastern Pacific Hermit Crab *Trizopagurus magnificus* (Bouvier, 1898) (Decapoda; Diogenidae), Reared in the Laboratory[1]

Anthony J. Provenzano, Jr.

ABSTRACT: Larvae were reared under various temperature conditions. Those maintained at 15°C were unable to moult to the second instar although some individuals lived as long as 35 days after hatching. At 20°C some individuals were able to reach fifth instar, but glaucothoes were obtained only at 25°C, 33–52 days after hatching. Effects of starvation and temperature on larval survival are discussed. The number of zoeal stages in the development of this species is variable, as it is in other diogenids which have been studied in the laboratory, glaucothoes of this species being obtained after four or five zoeal instars. Descriptions and illustrations of the zoeal stages and the glaucothoe are presented. No other larvae of this genus have been described and intra-generic comparisons of larval morphology were not possible, but a comparison was made of the zoeal and glaucothoe stages of this species with those of others in the family.

THE EASTERN PACIFIC contains a relatively rich hermit crab fauna but one which is still rather poorly known systematically. In spite of the great number of species which occur even in shallow waters from Alaska to the Equator, very little is known concerning the life histories or larval development of eastern Pacific hermit crabs. One of the first successful attempts to rear anomuran larvae in the laboratory was made by Hart (1937), who described larval stages of two species of *Pagurus* and one of *Paguristes* and of the mud shrimp *Upogebia*, all from British Columbian waters. Coffin (1960) studied another species of *Pagurus*. No papers describing development of any tropical eastern Pacific hermit crab have been published.

The genus *Trizopagurus* occurs in tropical seas around the world with the exception of the Caribbean (Forest, 1952). In the eastern Pacific, the genus is represented by *T. magnificus*, a not uncommon hermit crab of moderate size,

black with orange spots and orange antennae and antennules. The species was first described by Bouvier (1898) as *Clibanarius magnificus*, and was redescribed and illustrated by Boone (1932) as *Clibanarius chetyrkini*. Forest (1952) recognized it as belonging to his newly established genus. The species is distributed from the Gulf of California southward at least as far as La Plata Island, Ecuador, and occurs also in the Galapagos Islands, but nothing is known of its ecology. The limited data available from various systematic papers which have dealt with *T. magnificus* and the data accompanying specimens in various collections are sufficient to indicate that this species seems to prefer rocky areas, from the intertidal zone down to a few tens of meters. The female from which the larvae were obtained for the present study was collected in an area where the substrates consisted of rocky patches surrounded by mud. Species collected with *Trizopagurus* in this locality included *Dardanus sinistripes* Stimpson and *Clibanarius panamensis* Stimpson, both typical of inshore waters along the major part of the range of *T. magnificus*. *C. panamensis* is most often found in brackish water and muddy areas, often close to mangrove shores. Also collected with adults of *T. magnificus* were a species of *Isocheles*, about which virtually

nothing is known, and a specimen of an undescribed species of *Clibanarius*.

In recent years there has been an increasing amount of effort to study the larvae of the several families of hermit crabs especially to obtain ontogenetic information useful in classification and phylogeny of the group. No larvae of the seven currently recognized species of *Trizopagurus* have been studied previously. The purpose of the present work is to provide descriptions of the zoeae and glaucothoe of this tropical eastern Pacific hermit crab based on laboratory reared specimens, and to make available the limited ecological data obtained incidental to the rearing experiments.

ACKNOWLEDGMENTS

METHODS

Several females were collected in January 1964 by F. M. Bayer and R. Chesher at several intertidal localities near Venado Island in the Bay of Panama off the Canal Zone. One female *Trizopagurus magnificus* retained her eggs during passage back to Miami and yielded larvae during 16–18 January 1964. The temperature of the running sea water in which the female was kept was less than 20°C for one week prior to hatching and was 18°C during the hatching period. More than 800 larvae were obtained from this hatching and were placed in plastic compartmented trays as described in previous papers (Provenzano, 1962*a*; Provenzano and Rice, 1964), 1–10 larvae per compartment. Trays to which no food was

added were placed in four experimental temperatures (10°, 15°, 20°, and 25°C) to determine survival time of starved larvae. Additional trays, to which *Artemia* nauplii were added as food for the zoeae, were placed at the same temperatures. The three lower temperatures were maintained by thermostatically controlled refrigerators with fans to circulate air within the cabinets so that temperatures during the experimental periods did not vary more than ±0.1°C. For the highest temperature an air-conditioning unit in the culture room kept air temperature at 25°C ± 1.5°C.

Two lots of filtered sea water were used during the experiments, 32.6 parts per thousand from 16 January–3 February and 35.7 parts per thousand from 3 February to termination of the experiments.

Specimens and exuvia were preserved in alcohol or formalin. Specimens were cleared in 3–5% KOH and whole specimens and exuvia were dissected after staining with Mallory's acid fuchsin red, lignin pink, or chlorozol black, and were mounted. Study sketches were made with a Bausch & Lomb microprojector, and details were checked under higher magnification using a Tasco compound microscope. Final drawings were made with the aid of a Wild binocular M-5 dissecting scope equipped with a camera lucida.

The term stage is used herein in the sense of instar or intermoult.

All scales in the illustrations represent 0.5 mm. Carapace length of zoeae was measured from the tip of the rostrum to the most posterior lateral margin of the carapace, not to the dorsal posterior margin. Total length was measured from tip of rostrum to the median posterior margin of the telson exclusive of telson spines. Because of the flexible nature of the abdomen, the total length is less reliable a measure than the carapace length, which is based on a rigid structure. In the glaucothoes, shield length was measured from the tip of the rostrum to the cardiac suture. Carapace length was taken from the tip of the rostrum to the dorsal posterior transverse margin, and total length was measured from the tip of the rostrum to the posterior margin of the telson exclusive of setae.

The female from which the larvae were

hatched has been deposited in the U. S. National Museum (Catalog No. 113559).

Effect of Starvation at Various Temperatures

In order to determine the maximum survival time for unfed animals, several trays of larvae without food were placed in each experimental temperature. At 25°, 20°, and 15°C, 7–8 days were required for 50% mortality of the 54 starved larvae in each temperature, but at 10°C only 3 days were required for 50% mortality of 36 larvae. At 25°C, total mortality of the starved group required 10–12 days; at 20°C, 9–11 days; at 15°C, 8–10 days; and at 10°C all larvae were dead by the sixth day after hatching.

Survival at Various Temperatures of Larvae Fed with Artemia

At 10°C, 36 larvae were placed two per compartment. They began dying on the third day and by the seventh day all were dead. At 15°C, 145 larvae were placed one, two, or five per compartment. None moulted to stage II. By 21 days after hatching, approximately one-half had died, but a few survived as long as 35 days, then died in stage I.

At 20°C, 329 larvae were placed in trays, one, two, four, or more per compartment. Most moulted to stage II within 13–18 days after hatching, but a few lived to stage III. None became glaucothoe, but three specimens lived to stage V and died at approximately 85 days after hatching.

At 25°C, 305 larvae were placed in trays, one, two, or four per compartment. Nearly all survived the first moult, which took place 7–8 days after hatching. Glaucothoes were obtained at this temperature in as few as 33 and as many as 52 days after hatching. Only 18 glaucothoes were obtained. One specimen spent 23 days as a glaucothoe, then died in the moult to first crab stage, 56 days after hatching.

CAUSES OF MORTALITY

At 10°C the mortality of fed animals paralleled quite closely that for starved animals, indicating either that, despite presence of food,

the animals were unable to feed or that the temperature alone was sufficiently low to kill the animals directly. Even at the higher temperatures starved larvae did not swim during the last few days. Hence we may suppose that in nature larvae unable to feed within the first few days after hatching seldom survive as long as they did in these experiments, but nothing is known of the capacity of larvae to resume feeding and normal growth after varying periods of starvation. The shorter survival time at lower temperatures indicates that, at least at temperatures below 25°C, the exhaustion of yolk reserves was not the factor causing death among starved larvae, but that temperature had a direct negative effect on survival.

Because of the large number of larvae hatched and the limited time available to tend to them, some were placed together in compartments. It is unlikely that crowding was a primary cause of mortality since each compartment contained 40–60 ml of water and, in a few compartments in which as many as 10 larvae were together, survival was better than in many others with fewer animals. There was no apparent negative effect of crowding on survival.

It is obvious that the temperatures used were mostly below the satisfactory range for this species. At 10°C the larvae could not swim and died very quickly even though they had been gradually reduced to that temperature from the hatching temperature of only about 18°C. At 15°C the larvae were below the temperature at which normal development must take place, since none of them were able to moult. The fact that some lived as long as 35 days indicates that a few must have been able to feed at least occasionally even at that temperature, for starved larvae at 15°C were all dead by the tenth day after hatching. Even at 20°C larvae were apparently under very marginal conditions, since only three out of 329 lived to stage V.

At 25°C, although the percentage of survival to metamorphosis was low (18 glaucothoes were obtained from 305 original larvae), and although none of the glaucothoes actually survived to crab stage, the temperature was probably satisfactory, if still less than optimal. Contributing to the high mortality under laboratory conditions at 20° and 25°C

was an infection by a filamentous fungus-like organism which has occasionally struck experiments in the laboratory but which has not been identified. It is unfortunate that higher experimental temperatures were not available at the time. The 7–8 days required to reach the first moult at 25°C is approximately the same amount of time as is required by some other tropical species of hermit crabs in the laboratory, but is longer than for others. This period would almost certainly be shortened by several days at still higher temperatures.

DESCRIPTION OF THE LARVAL STAGES

There may be four or five zoeal instars in the development of *T. magnificus* prior to the glaucothoe stage.

General Features of the Zoeal Stages

The rostrum is long, exceeding the cephalic appendages, rather broad and deep, with the tip slightly curved ventrad. Each of the anterioventral corners bears a small blunt spine projecting anteriolaterally. The carapace bears no large spines posteriolaterally on the margins, but has numerous spinules which give the carapace a roughened appearance. These spinules extend onto the more posterior portions of the body as well, being especially noticeable on the dorsal surface of the abdominal somites and on the telson. As development proceeds, the spinules become relatively smaller until they are hardly noticeable in the last zoeal stage (Figs. 1 and 2). The telson is much broader than long in the first stage and in subsequent stages becomes progressively more elongate (Fig. 7).

The appendages are generally symmetrical throughout larval development, with occasional differences of one or two setae between one side and the other, but a notable exception is the pair of mandibles which are quite asymmetrical throughout the zoeal stages. Because zoeal mandibles have seldom been described or illustrated in detail, the functional and possible systematic significance of mandible armature is not well understood. Therefore both mandibles of each stage of this species have been illustrated from two aspects.

The zoeal stages have a yellow-orange overall color. Some of the parts of the exoskeleton,

notably the tip of the rostrum and the ends of the antennules, are yellowish but not from chromatophores. The carapace has a very diffuse yellow-orange color, also apparently not due to chromatophores. There are orange-red chromatophores laterally under the anterior half of the carapace, and others deep in the body at the bases of the maxillipeds, and there is a very large orange chromatophore on each side of the fifth abdominal somite near the base of the lateral spines. There are two pairs of similar large orange chromatophores anteriorly on the telson. Red chromatophores are found at the base of the antennae, on the labrum, and perhaps on the bases of the mandibles. A pair of red ones occurs on the first abdominal somite.

First Zoea

CARAPACE LENGTH: 1.4–1.6 mm
TOTAL LENGTH: 2.7–2.9 mm (3 specimens)

The first larval instar, as is typical of hermit crab larvae generally, has the eyes fused to the carapace. The sixth abdominal somite is fused to the telson, which bears the normal complement of 7 + 7 marginal telson processes, the outermost of which is a heavy spine, the second a delicate hair, while the others are articulated plumose setae.

The appendages of the first zoea (refer to figures) differ in no important respect from those of other species of hermit crabs at that stage (except that the well formed anteriolateral spine on the antennal scale is not always present in other diogenid hermit larvae and the medio-proximal corner of the basipodite of the first maxilliped has only setae, not a hooked process as in some other species of Diogenidae).

Second Zoea

CARAPACE LENGTH: 1.8–1.9 mm
TOTAL LENGTH: 3.5–3.8 mm (4 specimens)

The second larval instar differs from the first in many respects. The eyes are now free of the carapace and are stalked. The telson, while still fused to the sixth abdominal somite, has added a median pair of telson processes. All of the appendages have changed as shown in the figures.

The antennule has added some terminal aesthetascs, for a normal total of 6 or 7 terminal
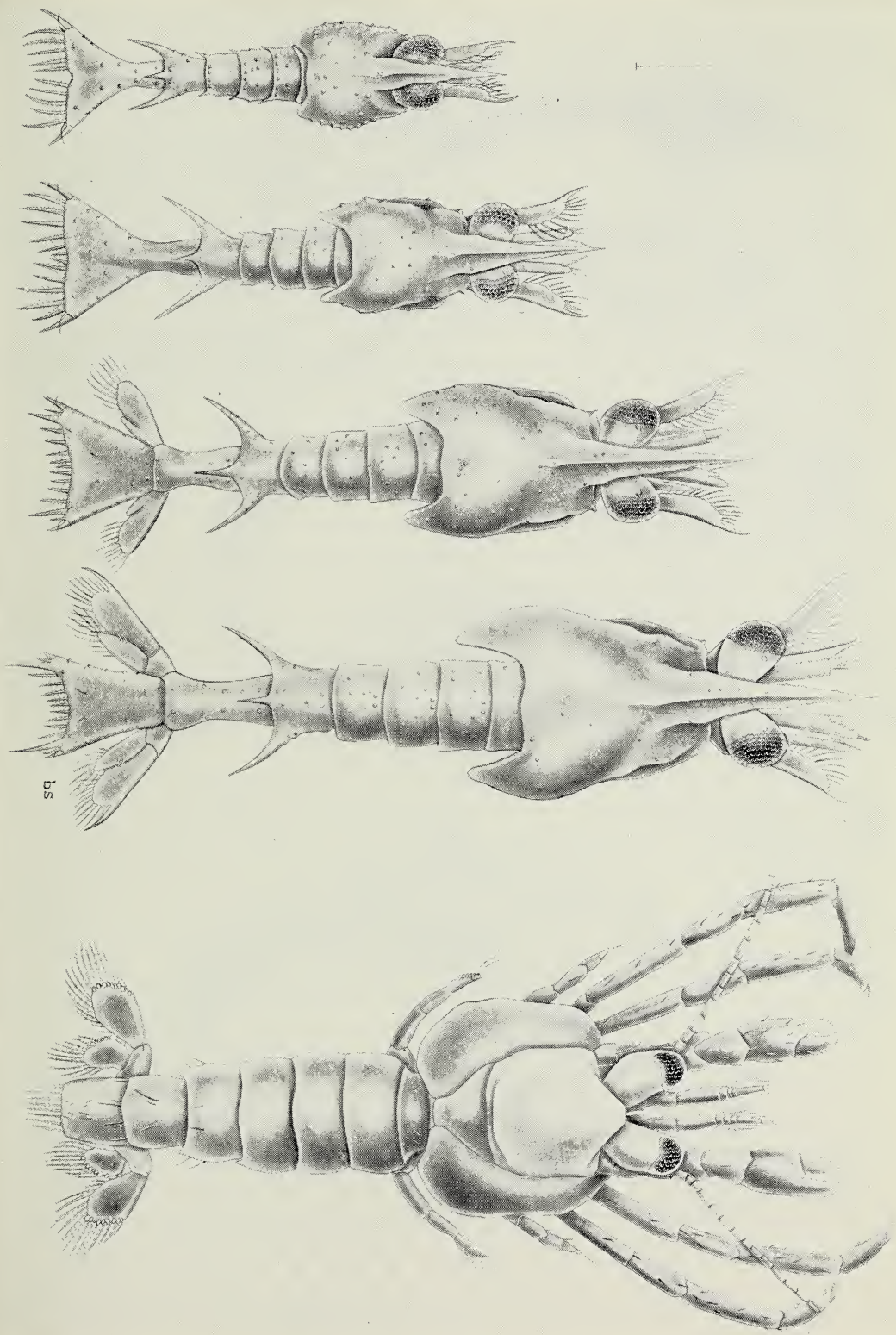
Fig. 1.   *Trizopagurus magnificus*. Dorsal views of the four zoeal stages and the glaucothoe.
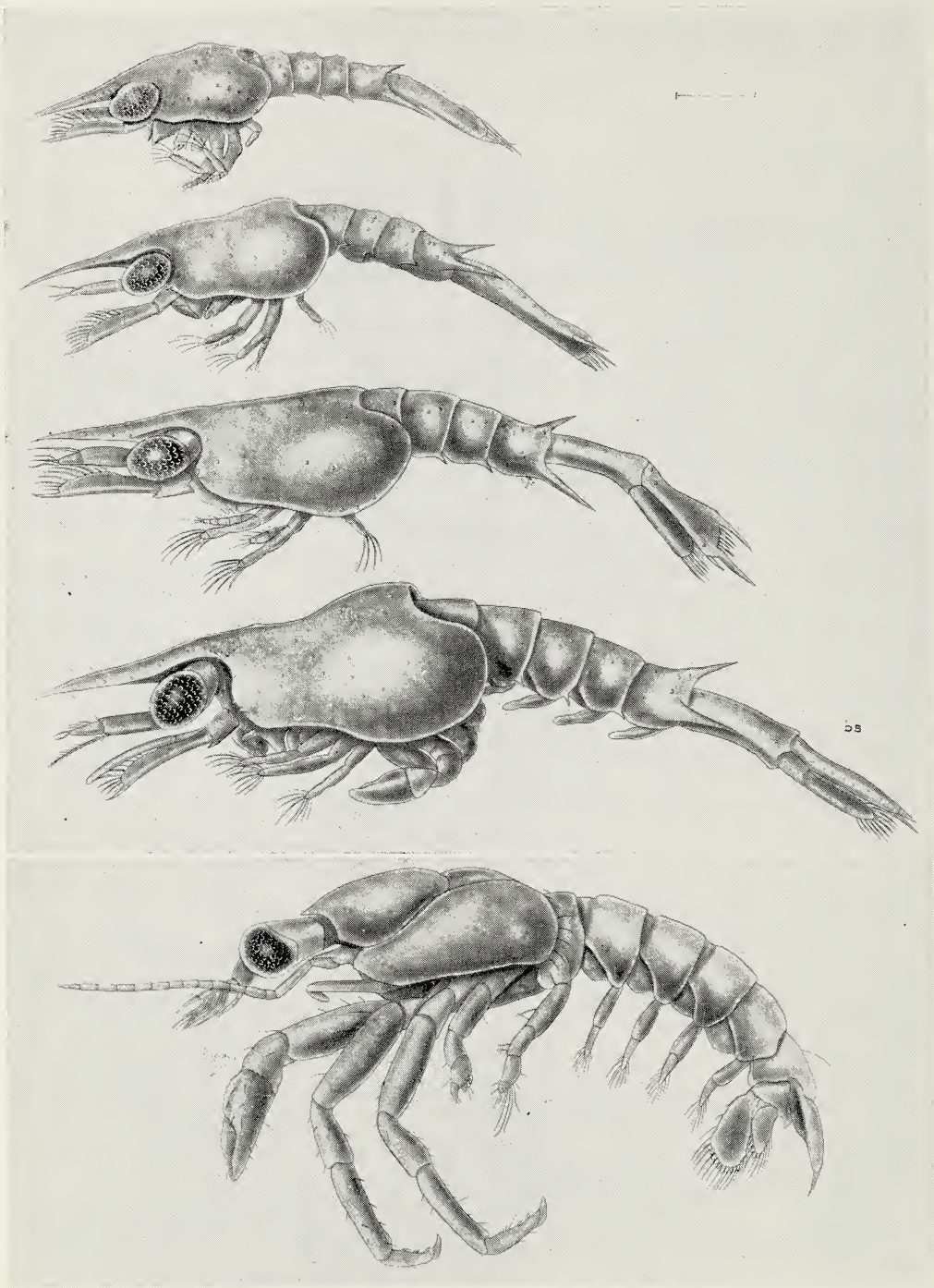
FIG. 2. *Trizopagurus magnificus.* Lateral views of the four zoeal stages and the glaucothoe.
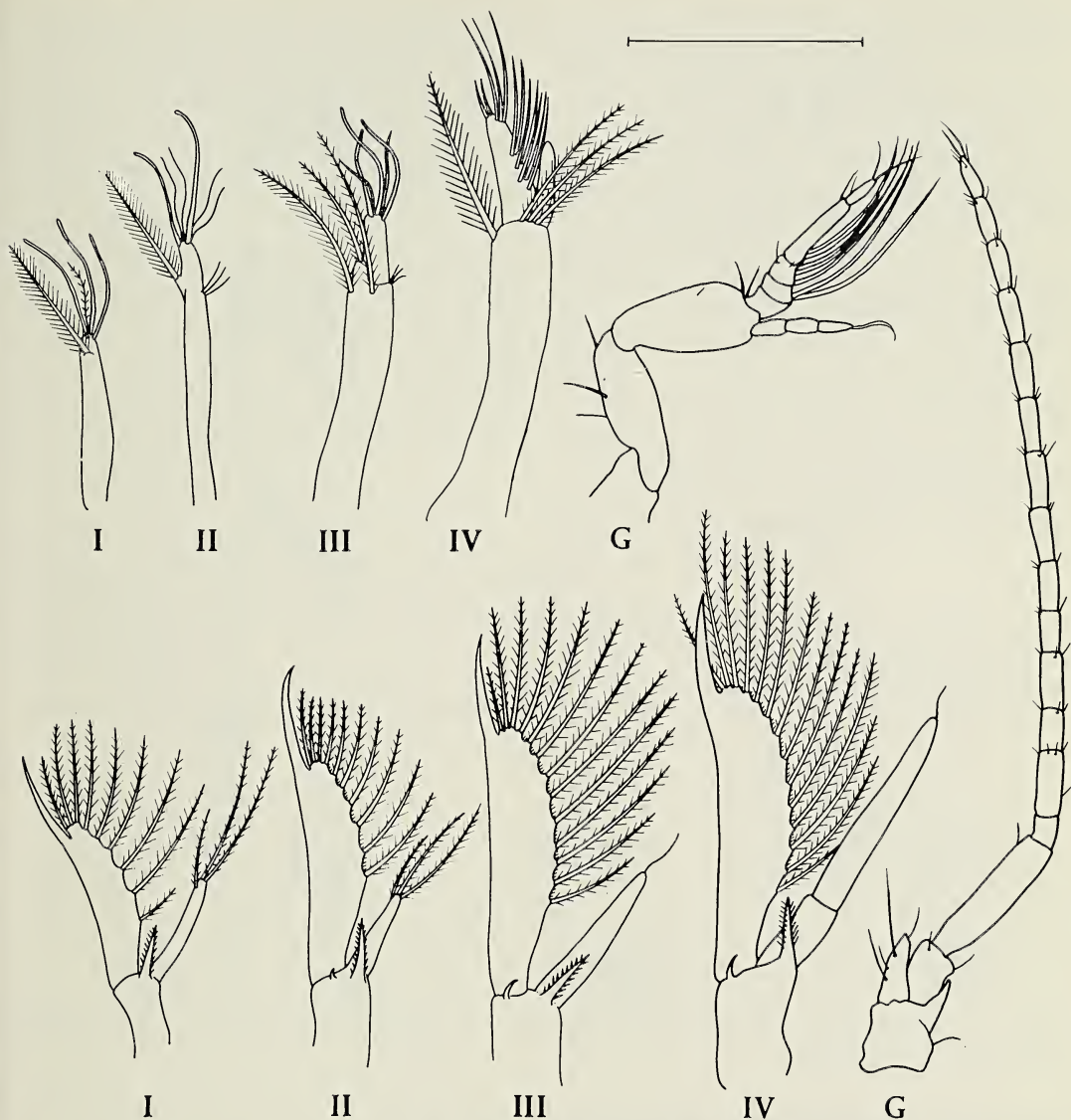
FIG. 3. *Trizopagurus magnificus. Top,* the antennule of zoeae I–IV and glaucothoe; *bottom,* the antenna of zoeae I–IV and glaucothoe.

processes and 3 subterminal setae at approximately the location of the future articulation of the rami.

The antenna has changed little, adding only a seta on the scale and a small tooth at the base of the scale.

The mandibles are not changed significantly.

The maxillule now has 4 strong teeth on the distal endite instead of 2. There may be a very short seta on the proximal segment of the endopodite, but usually it is not discernible.

The maxilla has added 1 or 2 setae to the scaphognathite and 1 or 2 setae to some of the basal and coxal endites.

The first maxilliped has added 2 natatory setae to the exopodite. The endopodite has lost the row of extremely fine setules on the lateral margins of the segments and has added to the three most proximal segments a single
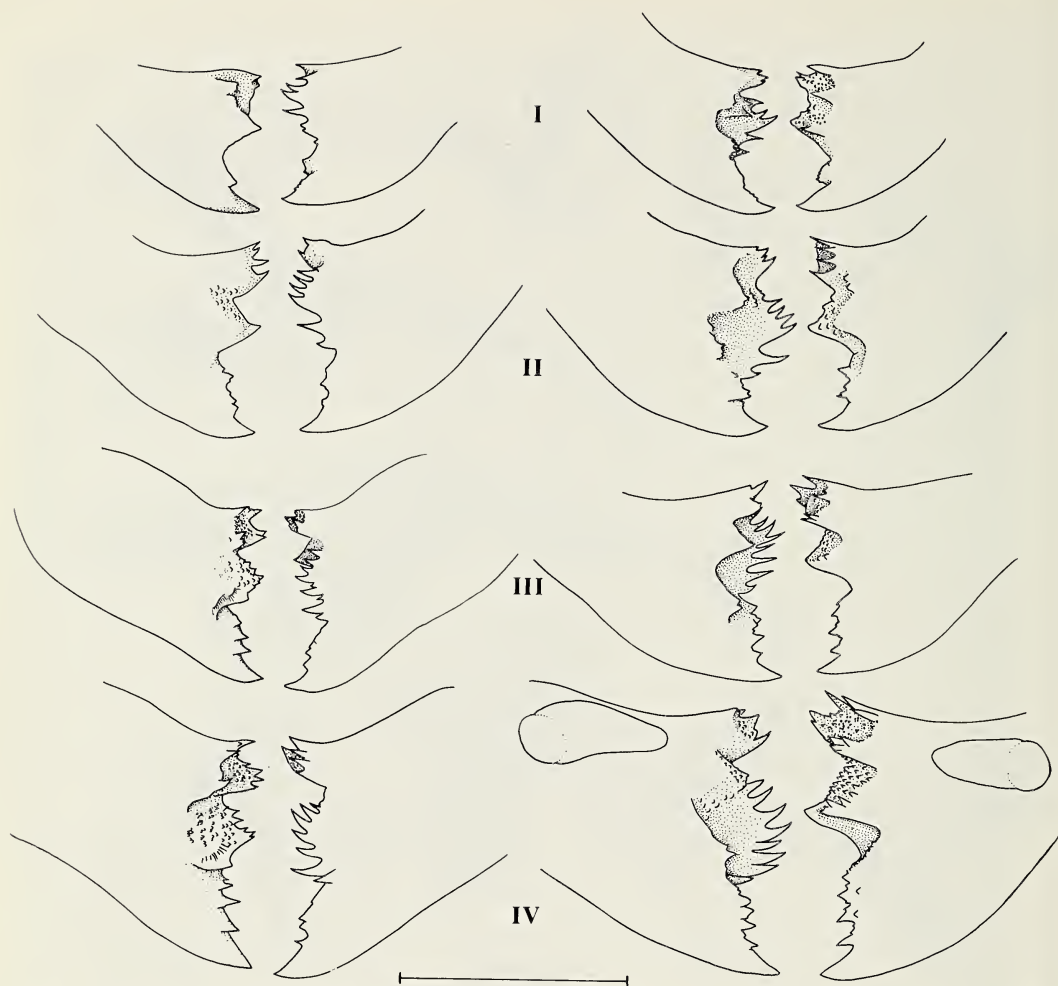
FIG. 4. *Trizopagurus magnificus*. The paired mandibles of zoeae I–IV. *Left column,* posterior surface; *right column,* anterior surface.

long plumose seta at the distal lateral margin. The appendage is otherwise basically unchanged.

The second maxilliped, like the first, has lost the fine row of setules on the endopodite, replacing them with long plumose setae on the two middle segments, and the exopodite has added 2 natatory setae.

The third maxilliped, a mere bud in the first stage but now functional, consists of a basipodite bearing an exopodite with 5 or 6 natatory setae. On the basipodite a lobe which will be the endopodite originates proximally and may bear a terminal seta.

Third Zoea

CARAPACE LENGTH: 2.15–2.40 mm (8 specimens)

TOTAL LENGTH: 4.25–4.55 mm (5 specimens)

The most obvious gross change is that the telson is now articulated with the sixth abdominal somite, and a pair of uropods has appeared. The posterior telson margin bears 8 + 1 + 8 telson processes, the median process being articulated and of the same type as the adjacent ones. However, the fourth process from each side is much enlarged, nonplumose, and is fused to the telson. There is

now a pair of fine plumose setae submarginally on the dorsal surface of the telson. The uropods consist of unarmed and nonarticulated endo-uropodites and setose exo-uropodites, each of which bears 8–10 marginal setae and 2 submarginal ones ventrally. There is a small ventral spine on the posterior margin of the sixth abdominal somite.

The antennule consists of a long peduncle with an articulated segment terminally which will be the dorsal flagellum. Proximal to the articulation there are 2 long plumose setae in place of 1 in the previous stages and 3–5 short simple setae. Usually there is evident a simple lobe which will become the ventral flagellum and which bears a plumose seta.

The antenna has 11–13 plumose setae on the scale and the endopodite (which has elongated considerably) has lost its 2 long and 1 short plumose setae and replaced them with a single terminal process which appears to be a single flexible seta.

The mandibles have added teeth.

The maxillule has 7 or 8 setae on the proxi-mal endite and now the tiny seta occasionally present on the proximal segment of the endopodite in earlier stages is missing.

The maxilla bears 9–11 plumose setae on the scaphognathite, the endopodite carries a total of 6 or 7 setae. The basal endites each carry 4 or 5 setae. The distal coxal endite may have 3–5, the proximal coxal endite usually has 8 or 9 setae.

The first maxilliped is basically unchanged but a third seta has been added to the medial margin of the proximal segment of the endopodite.

The second maxilliped is essentially unchanged.

The third maxilliped is little changed except for a slightly greater development of the endopodal lobe. The terminal seta of this lobe is sometimes missing.

Fourth Zoea

There is considerable variation in setation and relative degree of development of appendages in the fourth zoeal instar. Some individ-

I   II   III   IV

Fig. 5. *Trizopagurus magnificus. Top,* the maxillule of zoeae I–IV; *bottom,* the maxilla of zoeae I–IV.

I   II   III   IV

FIG. 6. *Trizopagurus magnificus. Top,* first maxilliped; *center,* second maxilliped; *bottom,* third maxilliped; of (*left to right*) zoeae I–IV.

uals, better developed than some of their siblings, were able to moult directly to the glaucothoe stage following this zoeal instar, but others, less developed, moulted into a fifth zoeal instar before the glaucothoe. In all fourth stages, however, the uropods are articulated with the sixth abdominal somite via a protopo-dite. Each exo-uropod now has a large fused spine at the posteriolateral margin and in addition may have 11–13 plumose setae marginally with 1–4 submarginally on the ventral surface. The endo-uropodites usually carry 5–7 marginal plumose setae and may have 1–3 submarginal setae ventrally. The telson itself is basically
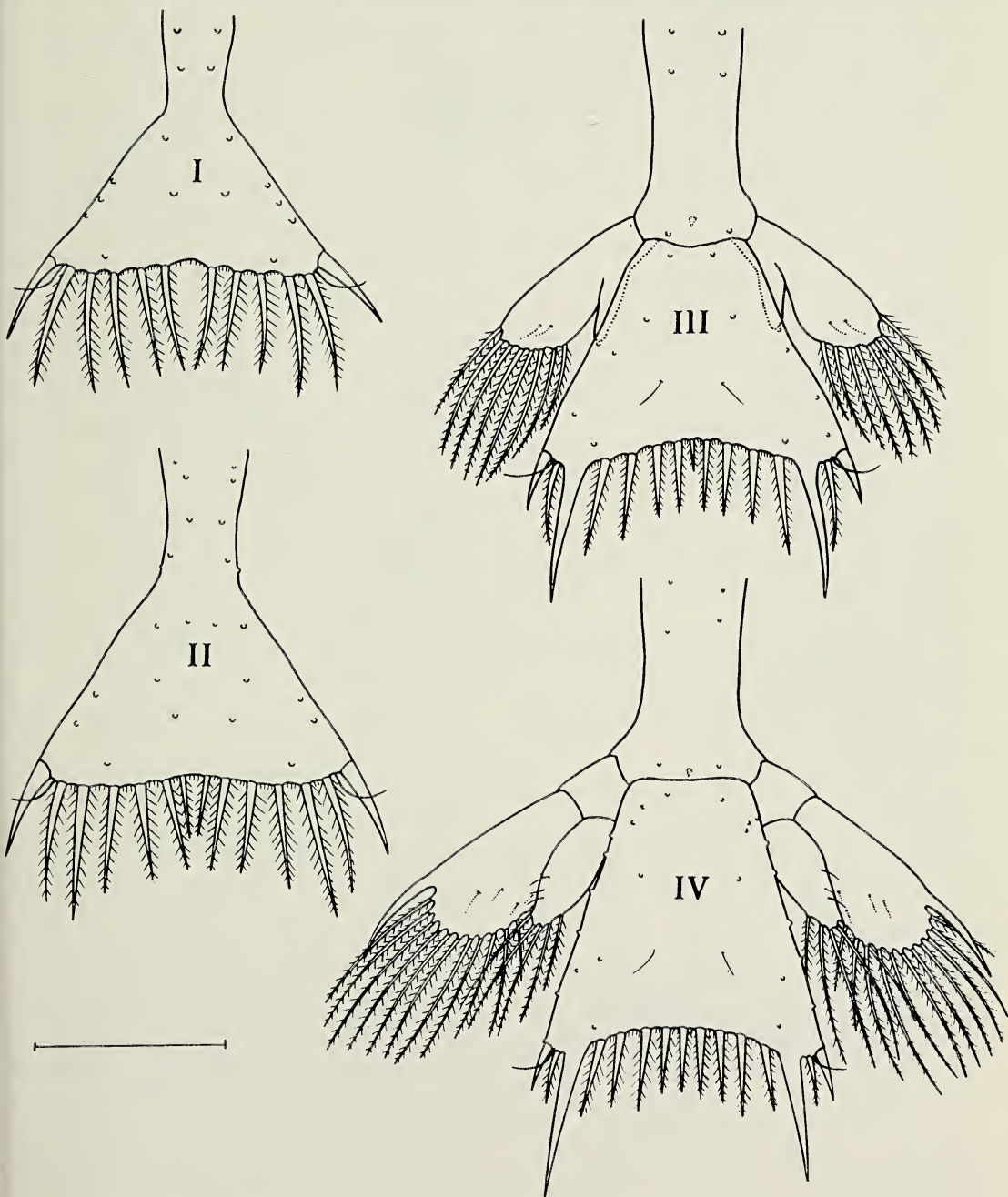
FIG. 7. *Trizopagurus magnificus.* Details of the telson of the zoeal stages.

unchanged from the previous stage except that it is more elongate and now may have either 1 or 2 pairs of submarginal setae. The medial telson process may be replaced by a pair of articulated processes. In series where the fourth zoeal instar was followed by another zoeal stage, the appendages were less well developed and the resulting fifth stage zoea did not differ significantly from the advanced fourth stage here described. The following remarks are based on specimens which moulted directly to glaucothoe from this stage.

Terminal Zoea

CARAPACE LENGTH: 2.4–2.9 mm (9 specimens)

TOTAL LENGTH: 5.5–6.2 mm (8 specimens)

The antennule shows subterminal groups of aesthetascs on the dorsal flagellum, and the lobe which will become the ventral flagellum is well marked and may have a terminal seta. There are 3 or 4 large plumose setae proximal to the distal articulation of the peduncle.

The antennal scale may have 13–15 plumose setae on the medial margin. The endopodite may now reach as far as the base of the terminal spine of the scale, is still terminated with a single process, but consists of at least 2 or 3 segments with one or more distinct articulations.

The mandibles are still more complex and show buds of the palps.

The maxillule has added 2 strong teeth on the basal endite, and usually 1 or 2 setae on the coxal endite.

A naked proximal lobe is present on the scaphognathite of the maxilla and as many as 22 plumose setae may be on the margin of the scaphognathite. The proximal lobe of the coxal endite of the maxilla has also increased in setation.

The first maxilliped usually carries 7, sometimes 6 or 8, natatory setae on the exopodite. The proximal medial corner of the basipodite may be rather prominently produced, with the usual pair of setae often reduced to a single seta.

The second maxilliped may have 7 or 8 natatory setae on the exopodite but is otherwise unchanged.

The third maxilliped has 7 or 8 (rarely 6)

natatory setae on the exopodite. The endopodite is very well developed, segmented, and bears a total of 1–5 setae on the terminal segments.

The pereiopods are well developed buds. The pleopods are represented by unarmed buds on abdominal somites 2–5.

Glaucothoe

SHIELD LENGTH: 0.9 mm (3 specimens)

CARAPACE LENGTH: 1.3–1.4 mm (2 specimens)

TOTAL LENGTH: 3.8–4.0 mm (3 specimens)

The post-zoeal stage in hermit crabs, as in all reptant decapods, is radically changed from the last zoeal stage: the long rostrum has disappeared, the carapace of the glaucothoe being almost the form of the juvenile, the pereiopods are free and functional, the pleopods are setose, the telson and all the cephalothoracic appendages have undergone radical change. The illustrations show how the gross external morphology of the glaucothoe of *T. magnificus* differs from the zoeal stages which preceded it.

As in all other described glaucothoes of the family Diogenidae, except that of *Diogenes pugilator,* there are no ocular scales at the bases of the eyestalks. In three specimens checked, the setation of the pleopods varied from 8–10 per pleopod, with no consistency in pairs or by somite. Other morphological features of particular significance are shown in the illustrations and will be discussed below.

The abdomen of the glaucothoe bears a few prominent chromatophores. In lateral view there is one red chromatophore anterior to the pleopods of the fourth abdominal somite. On the fifth abdominal somite there are two lateral and three ventral red chromatophores. Each of the protopods of the uropods, attached to the sixth abdominal somite, bears one red chromatophore. In dorsal view the fifth abdominal somite shows a pair of chromatophores on the anterior border and a pair on the posterior dorsal margin. The telson bears a pair dorsally and two pairs ventrally. Other chromatophores may be present, but only those mentioned above were noted in a brief examination of a living specimen. Diffuse orange color was seen under the eyestalks and in the region of the mouth, but the precise location of the origin of the pigment was not determined.
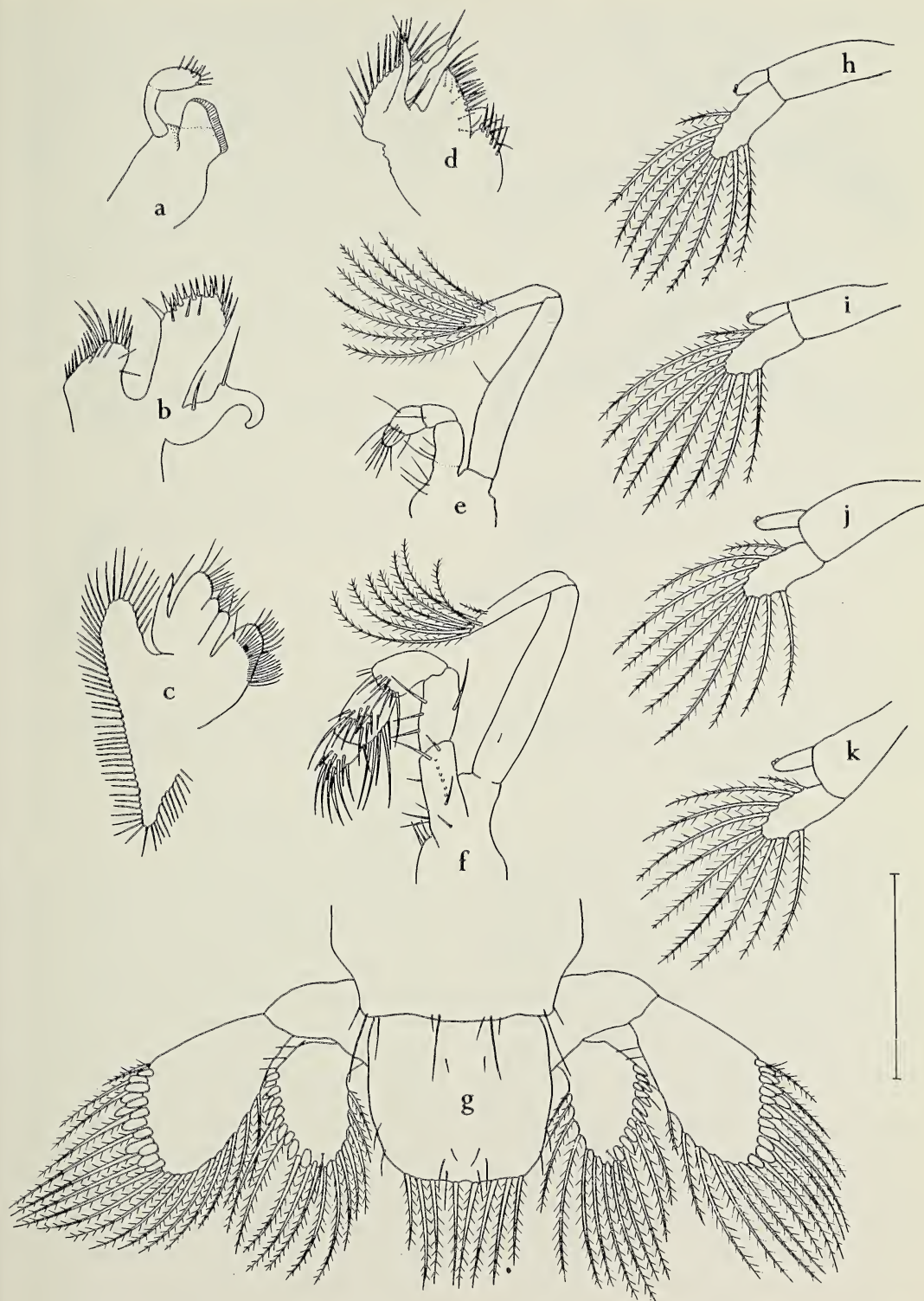
Fig. 8. *Trizopagurus magnificus*. Appendages of the glaucothoe. *a*, Mandible; *b*, maxillule; *c*, maxilla; *d*, first maxilliped; *e*, second maxilliped; *f*, third maxilliped; *h–k*, pleopods of abdominal somites 2–5; *g*, the tail fan. The posterior spine on the protopodite does not show in this view of the uropods.
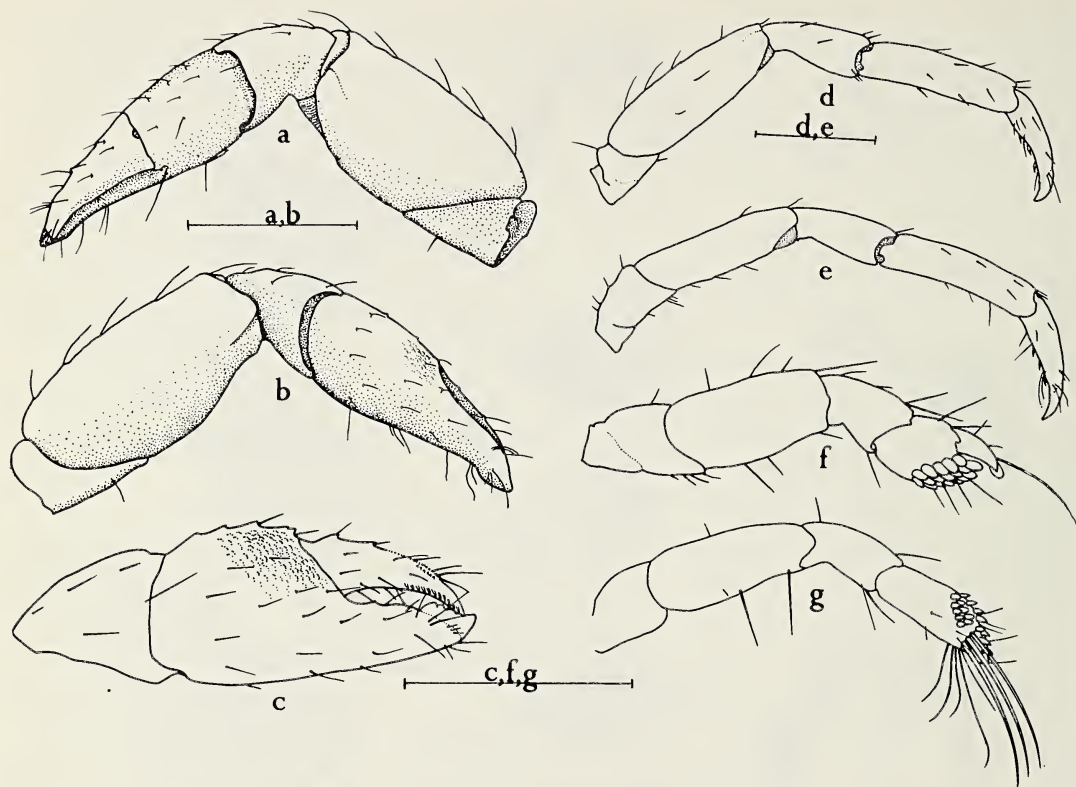
FIG. 9. *Trizopagurus magnificus*. Pereiopods of the glaucothoe, right side. *a,* Cheliped, medial view; *b,* same, lateral view; *c,* same, dorsal view, slightly enlarged; *d,* second pereiopod; *e,* third pereiopod; *f,* fourth pereiopod; *g,* fifth pereiopod.

DISCUSSION

Variability in the number of larval instars in anomuran development is now established as a widely occurring phenomenon. Species of Coenobitidae (Provenzano, 1962*a*), Diogenidae (Provenzano, 1962*b* and unpublished data), Galatheidae (Boyd and Johnson, 1963) and Hippidae (Rees, 1959) have been shown to have a variable number of instars in larval development of single species. Nor is this flexibility in development restricted to the anomurans. Caridean shrimps (Provenzano and Dobkin, 1962; Broad, 1957), scyllaridean lobsters (Robertson and Provenzano, unpublished), some brachyurans (Costlow, 1965; Yang and Provenzano, unpublished data), and at least one dromiid crab (Rice and Provenzano, 1966) have shown this pattern when reared in the laboratory. This phenomenon apparently results from the independence of the moulting

and growth processes and probably is of positive adaptive significance.

Although apparently there is not the uniformity in general appearance among larvae of the family Paguridae, as was thought only a few years ago, all described larvae of that family differ in certain features from larvae of the Coenobitidae and Diogenidae. The pagurid larvae which approximate most closely the diogenid larvae are those of the genu *Parapagurus,* some of which have been described by Dechancé (1964). The larvae of one species (Dechancé's sp. 1, which may be *P. pilosimanus* Smith), like those of *Trizopagurus magnificus,* have minute denticulations over at least parts of the body surface.

The only diogenid larvae which have been described as having any sculpturing on the cuticle are those of *Dardanus* as reported by Dechancé (1962), in which the cuticle was reported to have extremely small overlapping

scales with minute spinules. Larvae of a West Indian species, *D. venosus* (H. Milne-Edwards), have scutellations only on the rostrum in advanced stages and these scales are seen only with great difficulty, even under high magnification (Provenzano, unpublished data), but in that species there are minute tubercles distributed over the carapace and abdomen. These tubercles, much resembling those of *Trizopagurus* larvae, are more readily apparent in the early stages and, as development progresses, they become less apparent, as in *T. magnificus*. With this exception, *T. magnificus* is the only diogenid thus far known in which the larvae are so obviously ornamented that at least in the early stages the sculpturing is sufficiently obvious that it aids in identification. Perhaps this sculpturing will prove to be a generic character, but otherwise it is not possible yet to designate any single feature of these larvae of *T. magnificus* as being generically distinctive.

Since this is the first species in the genus *Trizopagurus* for which the larvae have been studied, it is not possible to compare these presently described stages with congeneric larvae from other parts of the world nor to point out which features may be reliable as specific *versus* generic characters. Moreover, since *T. magnificus* is the first species of Diogenidae of the tropical eastern Pacific for which a description of the larval stages is now available, it is not possible to offer a list of characters by which larvae of this species can be separated with certainty from other diogenid larvae with which they might occur in plankton.

The enlargement and fusion to telson of the fourth telson process in the third and fourth zoeal stages of *T. magnificus* is found in the two species of *Calcinus* which have been studied, in *Dardanus arrosor,* and in the land hermit crab *Coenobita clypeatus*. None of the three species of *Paguristes* so far studied show any change in this process in their zoeal stages, but since there are at least 25 species of *Paguristes* in the West Indian faunal region alone, and probably well over a hundred world-wide, this character may show some variation. In *Clibanarius* and *Diogenes* there is fusion of this process, but instead of enlargement there is reduction, even approaching apparent absence.

Some characters, such as the spine of the antennal scale, may vary in size within a particular genus (see Dechancé, 1962: Fig. 3), and hence may be of little value as an indicator of genus but may be reliable as a specific character. The mediodorsal spine of the fifth abdominal somite in *Trizopagurus* is not known to occur in larvae of *Clibanarius* or *Dardanus,* but may be characteristic of *Coenobita* and of *Calcinus, Diogenes,* and at least some species of *Paguristes,* while the posteriolateral spines on that somite usually are found in these latter genera and in *Dardanus* as well.

In combination, the characters which distinguish the larvae of *T. magnificus* from all other described diogenid larvae are: the peculiar surface sculpturing, the trio of large spines on the fifth abdominal somite (shared with several genera, but not with *Dardanus* or *Clibanarius*), and the absence of the posteriolateral carapace spines which apparently characterize *Calcinus*.

In addition to *Coenobita, Calcinus, Clibanarius,* and *Dardanus,* for which larvae have been described from other faunal regions, there are within the range of *T. magnificus* other related genera (*Cancellus, Aniculus, Allodardanus, Isocheles,* and *Petrochirus*) for which no larvae have been described from any part of the world.

The glaucothoe of *T. magnificus* is typical of the family Diogenidae in general features. As opposed to glaucothoes of the Paguridae, those of the Diogenidae (and of the Coenobitidae) are generally symmetrical (the aberrant genus *Diogenes* is an exception), the chelae being of subequal size, and the tail fan especially being similar in both sides. The uropods in Diogenidae and Coenobitidae have well developed, functional endopodites, whereas in Paguridae the endopodites are very much reduced.

This glaucothoe differs in many respects from those known from other faunal regions and it is reasonable to expect that these features will be of value in separating planktonic *T. magnificus* glaucothoes from those of other hermit crabs in the eastern Pacific when the latter have been studied.

With respect to described glaucothoes of non-pagurid hermit crabs, that of *T. magnificus*

differs notably from that of the West Indian *Coenobita clypeatus* in having a well developed exopodite on the third maxilliped and in not having an extremely long terminal seta on the antennal flagellum (both the reduced exopodite and the long terminal seta probably are generic or familial characters of the land hermit crabs (Provenzano, 1962a). The glaucothoe of *T. magnificus* differs from those of the Pacific *Dardanus scutellatus* and the West Indian *D. insignis* and *D. venosus* (Provenzano, 1963a, 1963b) in size (all of which are much larger), in eye shape (in *Dardanus* the cornea is wider than the eyestalk, not narrower), in not having their peculiar armature of the ambulatory dactyls, in having a shorter telson, and in having a reflexed palp on the endopodite of the maxillule, which those species lack. The glaucothoe attributed to the West Indian *Petrochirus diogenes* (Provenzano, 1963b) was erroneously identified (Provenzano, in preparation), but the true glaucothoe of *Petrochirus* (a genus represented in the eastern Pacific by *P. californiensis*) probably differs from that of *Trizopagurus* in those same features as does *Dardanus*.

The glaucothoe of *Clibanarius erythropus* from the Mediterranean (Dechancé, 1958) differs from that of *T. magnificus* in being smaller, in having a suboval telson, in lacking a prominent spine on the protopodite of the uropod, in having a smaller number of segments on the antennal flagellum, and in details of setation. The four species of *Paguristes* for which glaucothoes have been described, *P. turgidus* Stimpson, from the northeastern Pacific (Hart, 1937); *P. oculatus* (Fabricius), from the Mediterranean (Issel, 1910 and Pike and Williamson, 1960); *P. abbreviatus* Dechancé, from the western Indo-Pacific (Dechancé, 1963); *P. sericeus* A. Milne-Edwards, in the West Indies (Rice and Provenzano, 1965), all differ from that of *T. magnificus* in having longer dactyls on the second and third pereiopods, in armature of the chelipeds, in having a very small number of segments in the antennal flagellum (8 segments or less), and in having only 2 segments in the ventral ramus of the antennule. Glaucothoes of *Calcinus*—specifically, *C. ornatus* (Roux), in the Mediterranean (Pike and Williamson, 1960); and *C. tibicen*

(Herbst), in the West Indies (Provenzano, 1962b)—apparently bear closest resemblance to that of *T. magnificus*, but when the eastern Pacific glaucothoes of *Calcinus* have been studied, probably there will be size differences and details, such as armature of the protopodite of the uropod, by which these forms may be distinguished.

An apparently unique feature of the glaucothoe of *T. magnificus* is the patch of granulations on each chela.

The only other diogenid genera occurring in the range of *T. magnificus,* and for which no glaucothoes have been described from other regions, are *Allodardanus* (*A. bredini* Haig and Provenzano, 1965), *Isocheles* (several species), *Aniculus* (*A. elegans* Stimpson) and *Cancellus* (*C. tanneri* Faxon). In *Allodardanus* and *Isocheles* the dactyls of the second and third pereiopods are rather long, and it is likely, though not certain, that the glaucothoe will show the same condition. Both *Aniculus elegans* and *Cancellus tanneri* have very short dactyls, but neither species has a reflexed palp on the endopodite of the maxillule, and so their glaucothoes should be distinguishable from that of *Trizopagurus*.

Particularly important characters for the future discrimination of diogenid glaucothoes should be the overall body size, the shape and armature of the telson, the armature of the protopodite of the uropods, the shape of the eyes, the relative lengths of the dactyls and propodi of pereiopods two and three and the armature of these dactyls, the length of the setae on the antenna relative to lengths of antennal segments, presence or absence of a reflexed palp on the endopodite of the maxillule, and the armature of the chelipeds.

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Bathymetric Distribution of Chaetognatha, Siphonophorae, Medusae, and Ctenophorae off San Diego, California[1]

ANGELES ALVARIÑO

THE SAMPLES STUDIED were obtained at various depths with the BONGO or BMOC open-closing paired zooplankton net (McGowan and Brown, 1966), at 30°30′N, 120°00′W, from 27 August to 8 September 1965.

These collections were taken during night hours (27 August to 8 September 1965), and daylight hours (30 August to 5 September 1965). Quantitative data for each of the species were determined for each of the nets (left and right) for collections at the various strata surveyed; and variations in the number of specimens and in the species were observed at times in the same haul for the samples from the left and right nets. Diagrams were made showing the qualitative and quantitative distribution of the species in the two nets for each of the stratified hauls. However, in the final diagrams the medians for both left and right samples were plotted for each of the stratified hauls.

The data from the collections made at different times and depths during the same half day (dark or daylight) were plotted together. Since the hauls for the same half of the day were made on different dates (there was a lapse of time from one haul to the other), it is obvious that changes might take place at times, either in the depth at which the various species were found or in the quantity of individuals obtained.

In the case of the siphonophores, the necto-phores of a physonectes appeared in either the right or left net and in the other net the

pneumatophores with the nectosoma and siphosoma attached. Similarly, in other cases, one of the paired nets contained the bract or the superior nectophore and the other net the gonophores or the inferior nectophore of the eudoxid or paragastric forms of the Diphyidae.

The quantitative distribution of Chaetognatha and Medusae are noted in the diagrams; but in the case of the Siphonophorae, although data on the number of superior and inferior nectophores, gonophores, bracts, pneumatophores, etc. were obtained, because of the peculiar anatomical structure of these organisms it was not convenient to attempt a quantitative representation. In the case of the Monophyidae and Diphyidae, for instance, it will be easy to establish the number of individuals present from the part obtained in the sample, but this is not so for the Physophorae and Hippopodiidae. Therefore, only the qualitative distribution of the siphonophores was considered in preparing the final diagrams.

During each tow about 10,000 m³ of water were filtered through the net; thus the samples were directly and quantitatively comparable.

Collections were made at the following depths (in meters):

NIGHT	DAYLIGHT
100–10	110–0
100–20	350–250
300–235	460–0
460–410	525–401
500–420	1720–1340
620–530	2300–1880
775–685	2630–2210
840–690	3040–2620
1030–860	
1040–890	
1242–1090	
1710–1450	
2020–1800	
2170–1950	
2320–2100	
2460–2100	

Several gaps in the bathymetric distribution are obvious, since collections were not obtained at some strata. The most important sampling gap was in the daylight series, of about 800 m (1340–525 m), which interrupts the data on the bathymetric distribution. This lack of data, and the one haul from 460 m to the surface during the daylight series (considered only for the siphonophores), do not permit the location of the upper or lower limits of the distribution of several species.

Quantitative data were obtained by the method explained by Alvariño (1965c and 1966a).

The bathymetric zones considered are: epiplanktonic (upper 200 m), mesoplanktonic (200–1000 m), bathyplanktonic (below 1000 m). The vertical division into zones cannot be static, however, because the stratification of the organisms is controlled by bio-physicochemical factors.

CHAETOGNATHA

Figures 1 and 2 show the quantity of each of the species found and their distribution for the day and night series, respectively.

The epiplanktonic species observed here were: Krohnitta subtilis, Pterosagitta draco, Sagitta bierii, S. bipunctata, S. enflata, S. euneritica, S. hexaptera, S. minima, S. pacifica, S. pseudoserratodentata, and S. scrippsae. A typical mesoplanktonic species, S. decipiens, also was present in the upper 100 m, but extended to 620 m depth.

Other species characteristic of the mesoplanktonic levels which extended their distribution into the bathypelagic domain were: S. maxima, S. macrocephala, and S. zetesios. The bathyplanktonic species reaching various levels of the mesoplanktonic zone were: Eukrohnia bathypelagica, E. fowleri, and E. hamata.

During the nighttime collections, K. subtilis and S. scrippsae did not appear in the upper 100 m, but did appear at 500–235 m and 460–235 m, respectively. S. pacifica was absent from any level.

The species present in the upper 100 m layers for both night and daylight series, S. bierii, S. decipiens, S. euneritica, and S. pseudoserratodentata, were more abundant at night

than during daylight, whereas S. minima was more abundant during the day, and the others appeared within the same range of abundance for both periods.

The species spreading from the surface to 300 m depth during daylight were S. euneritica and S. pacifica, and at night, S. enflata and S. hexaptera, the latter appearing down to 525 m in the daytime.

Sagitta bierii populated the upper 100 m down to 500 m during both day and night, showing the greatest concentration in the upper 100 m and the lowest between 400 and 500 m at night, whereas during daylight the distribution was homogeneous along the layers it populated; but S. hexaptera presented the highest concentration from 300 to 235 m at night, and was homogeneous at daylight down to 525 m depth. K. subtilis extended during daylight from the surface to 525 m, with higher concentrations in the upper 100 m, whereas at night it was present only between 235 and 500 m.

The presence of S. decipiens in the upper 100 m both at night and by day appears to indicate that upwelling phenomena took place at this location. Two specimens of S. decipiens were observed in the left net for the tow from 2630 to 2210 m, and two specimens in the right net from 3040 to 2620 m during the day series. These showed evidence of contamination, however, and were omitted from the figures.

S. scrippsae extended during daylight from the surface to about 500 m, with maximum concentration at 350 to 250 m. At night it extended only from 235 to 460 m, with maximum concentration between 300 and 235 m.

The influence of light in the bathymetric distribution could be understood when observing the vertical distribution of S. bierii, S. decipiens, S. euneritica, and S. pseudoserratodentata. However, if the factor of light is responsible for the vertical migration of these organisms, it fails to explain the distribution of K. subtilis, S. enflata, S. maxima, and S. scrippsae.

Therefore, the factors influencing the vertical distribution and displacements of the species of chaetognaths may be of various kinds, and interacting: light, temperature, oxygen,
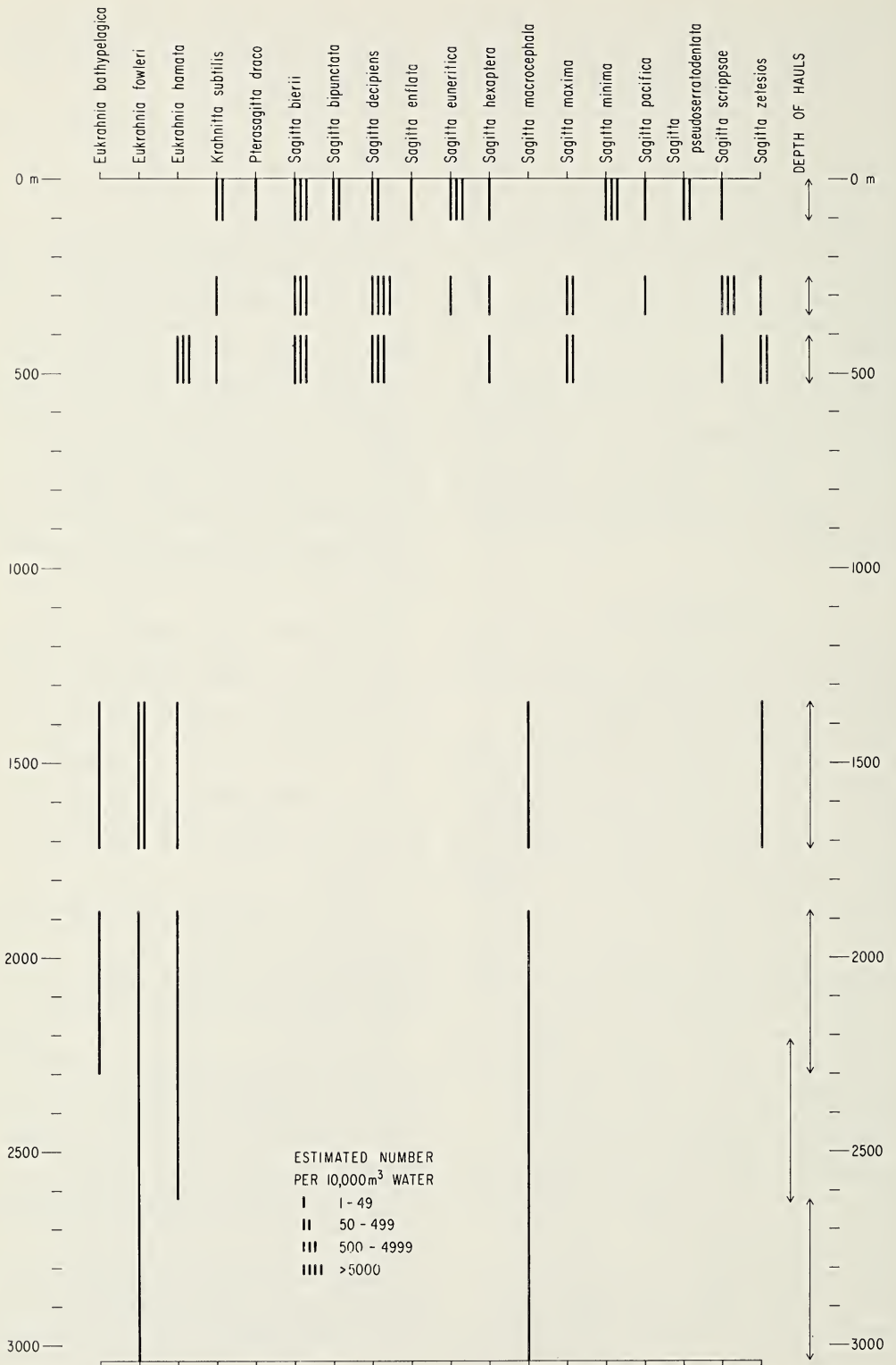
FIG. 1.   Bathymetric distribution of Chaetognatha during the daylight series.
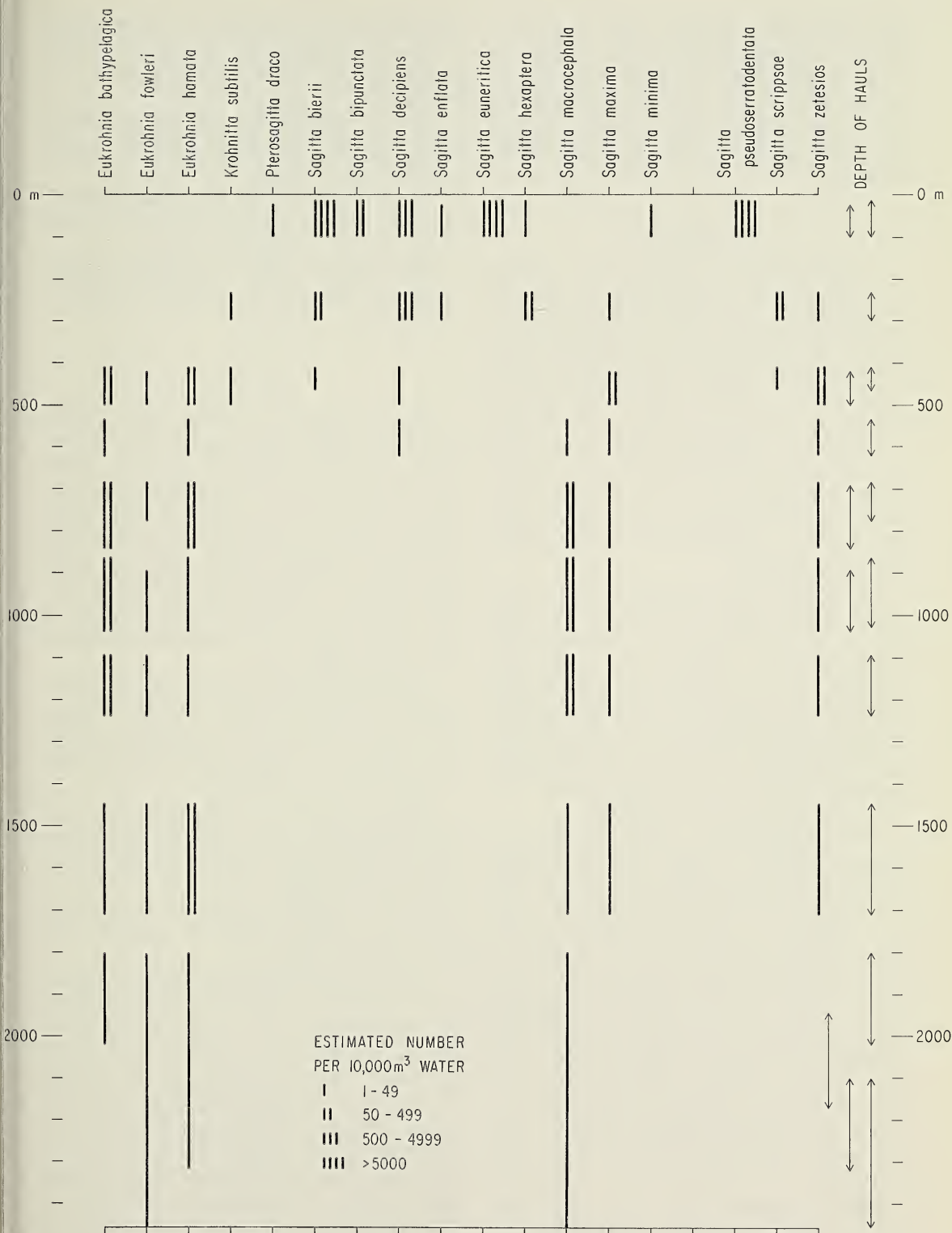
FIG. 2. Bathymetric distribution of Chaetognatha during the night series.

food, hydrostatic pressure, and bio-physico-chemical interrelations with other organisms of the pelagic realm. Also to be considered is the structure of the population, since young individuals appeared to be at levels closer to the surface than were adults (Alvariño 1964*a*, 1965*a*).

SIPHONOPHORAE

A greater number of species was observed in the upper 100 m in the daylight series than in the night (Figs. 3 and 4). The species observed in the upper 100 m for both series were *Muggiaea atlantica, Chelophyes appendiculata,* and *Eudoxoides spiralis.* These were joined in daylight by *Eudoxia russelli, Lensia hotspur, L. subtiloides, Amphicaryon acaule,* and *Stephanomia bijuga,* and only by *A. ernesti, L. multicristata* (extending also to the mesoplanktonic levels), and *Nectodroma reticulata* at night. The last two inhabited the mesoplanktonic domain in daylight.

The daylight haul from 460 to 0 m was included in the diagrams for the siphonophores only, to show the presence of several species at those levels. However, the bathymetric limits cannot be determined for some species; thus, the upper limit of the daylight distribution for *Chuniphyes moserae, Ch. problematica,* and *Heteropyramis maculata,* and both upper and lower limits for *L. challengeri* and *Nectodroma dubia,* are not yet established.

The mesoplanktonic species appeared in higher numbers at night than in daylight. Typical mesoplanktonic species such as *L. ajax, L. conoidea, L. grimaldii, Bargmannia elongata, Stephanomia rubra, Physophora hydrostatica,* and *N. dubia* were not observed at night; and *Nectopyramis diomedeae, N. thetis,* and *N. natans* were not observed in daylight. Species appearing in the mesoplanktonic levels at night which extend to deeper layers at daylight were *L. achilles, Vogtia kuruae,* and *Rosacea plicata. Dimophyes arctica* was obtained in the mesoplanktonic levels at night and only at the bathyplanktonic zone during daylight.

Species occupying both meso- and bathypelagic regions were *Ch. multidentata, Ch. moserae, Ch. problematica, Clausophyes galeata,*

Crystallophyes amigdalina, Heteropyramis maculata, L. achilles, L. hostile, L. lelouveteau, L. reticulata, and *Nectodroma reticulata* (in daylight).

Species observed at the bathyplanktonic levels only were *Clausophyes ovata, Ceratocymba dentata,* and *L. havock.*

One specimen of *Velella* (longest axis 70 mm, and sail oriented NW–SE) was obtained with a dip net, 8 September 1965.

One complete colony of *Physophora hydrostatica* was obtained in daylight at depths of 350–250 m.

MEDUSAE

Higher numbers of species were observed during the night series than in the daytime (Figs. 5 and 6). *Liriope tetraphylla* was the only species found for both series in the upper 100 m, presenting a higher number during daylight. *Sibogita geometrica* and *Cunina peregrina* were observed only at night and in the upper 100 m. *Phialidium discoidum* and *Crossota alba* were observed during daylight in these upper strata, and extended from 685 to 1030 m at night.

The mesoplanktonic species were *Sarsia coccometra, Zanclea costata, Pandea violacea, Heterotiara anonima, Colobonema sericeum, Crossota alba, C. brunnea* (extending deeper at night), and *C. pedunculata.*

Species populating both the meso- and bathypelagic levels were *Halicreas papillosum, Atolla wyvillei,* and *Periphylla hyacinthina* (observed only at night).

Medusae observed exclusively at the deepest levels were *Homeonema alba, Aegina citrea,* and *Nausithoe rubra.*

The medusae showed some degree of stratification related to the size of the specimens; thus individuals of *A. wyvillei* 12–30 mm in diameter appeared at 300–235 m, whereas specimens 75 mm in diameter were found at 1710–1450 m. However, specimens up to 100 mm in diameter were obtained in the 620–530 m level. The size-stratifications for this species appeared to be more clear-cut during the daylight series, when individuals 7–20 mm in diameter appeared in the 460–410 m level, and those 30–60 mm in diameter at 1720–1340 m.
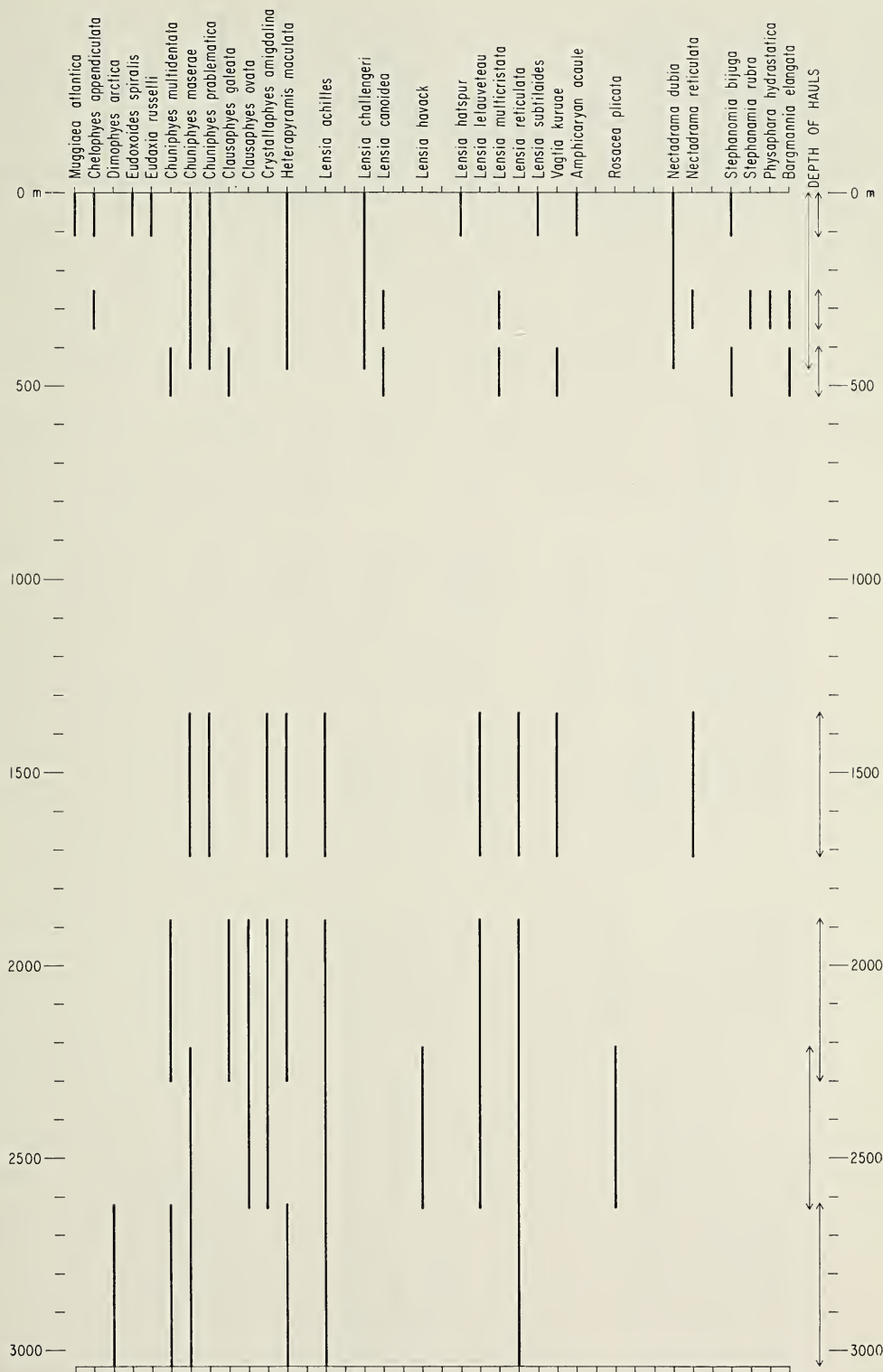
FIG. 3. Bathymetric distribution of Siphonophorae during the daylight series.
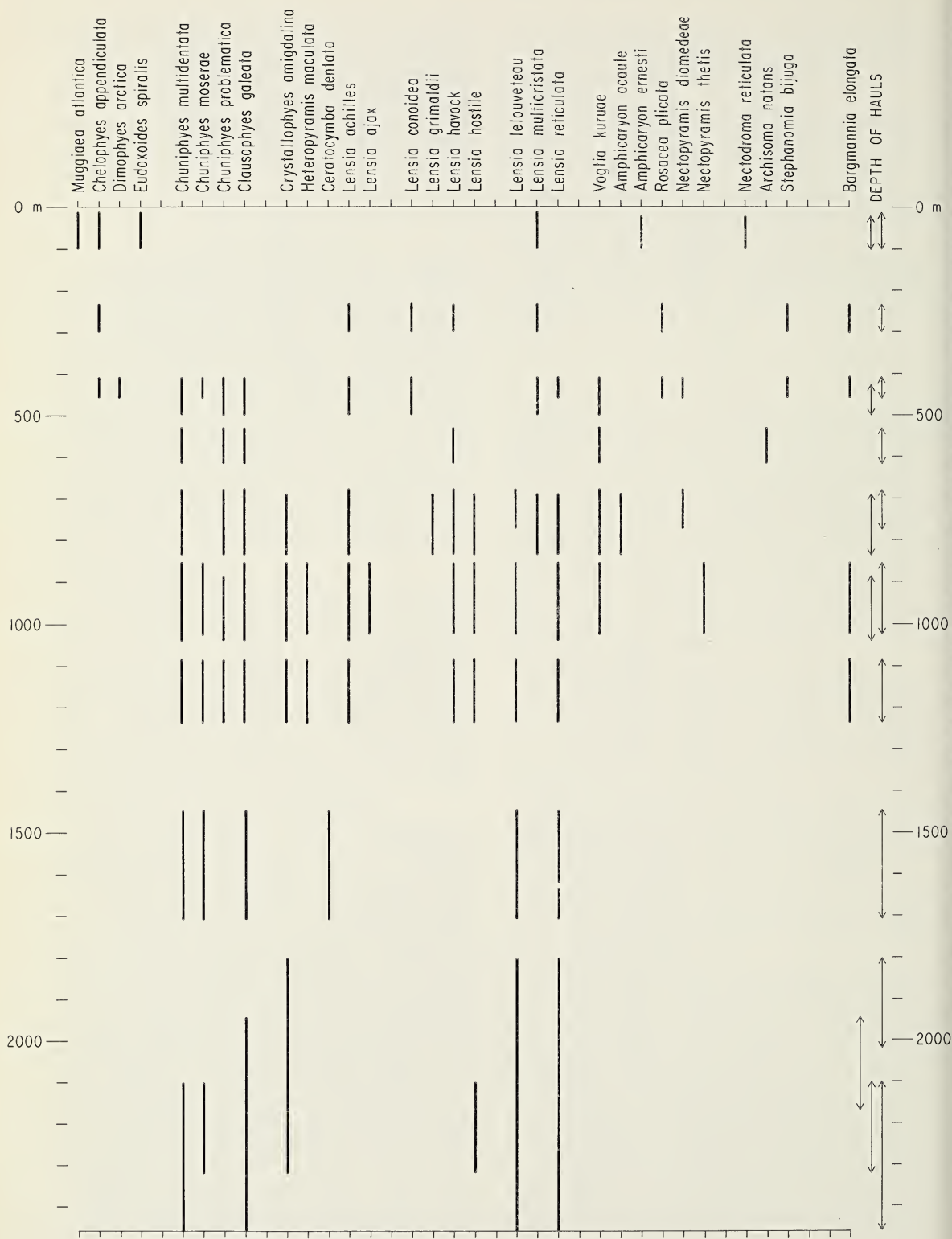
FIG. 4. Bathymetric distribution of Siphonophorae during the night series.
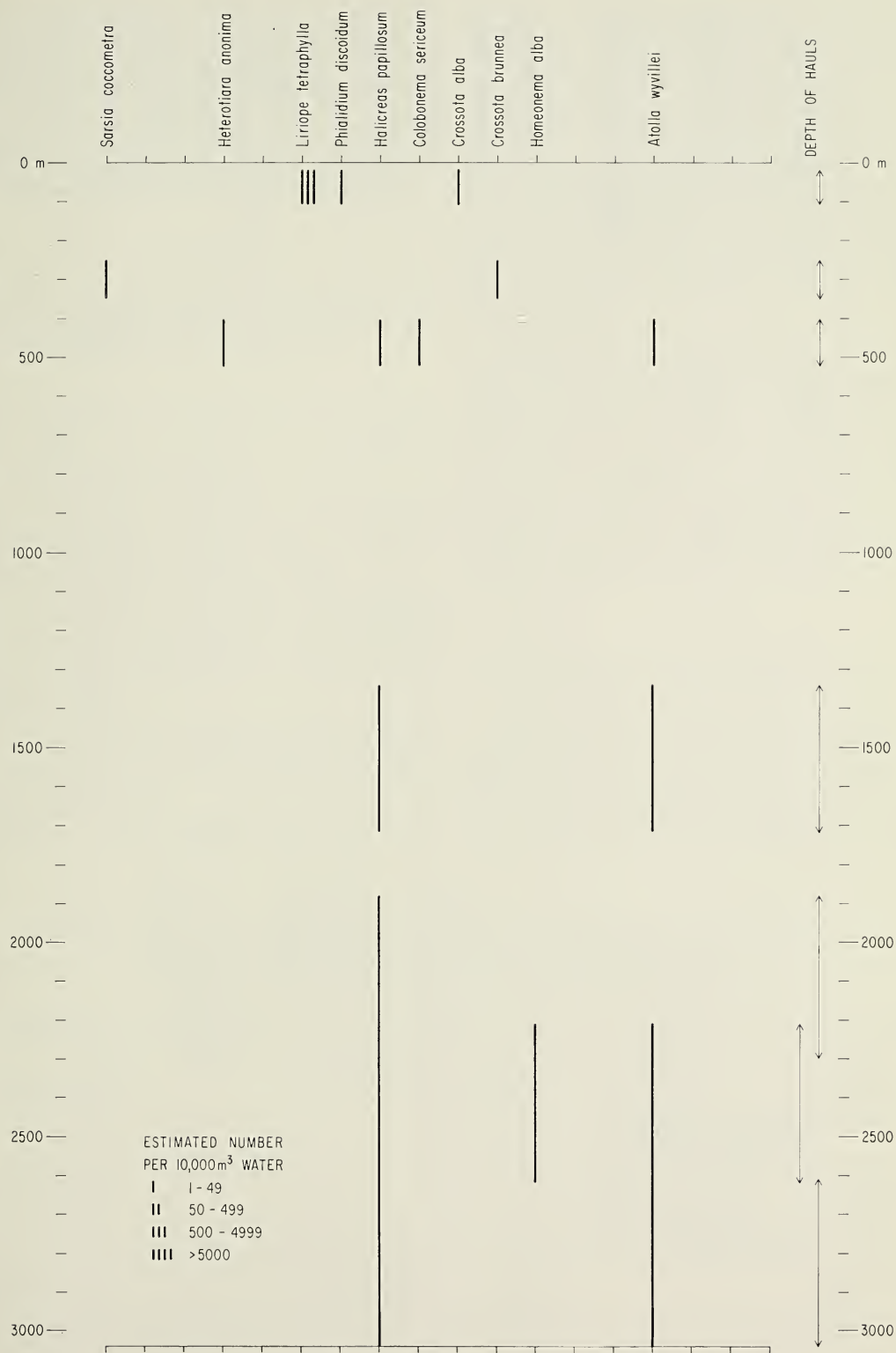
Fig. 5. Bathymetric distribution of Medusae during the daylight series.
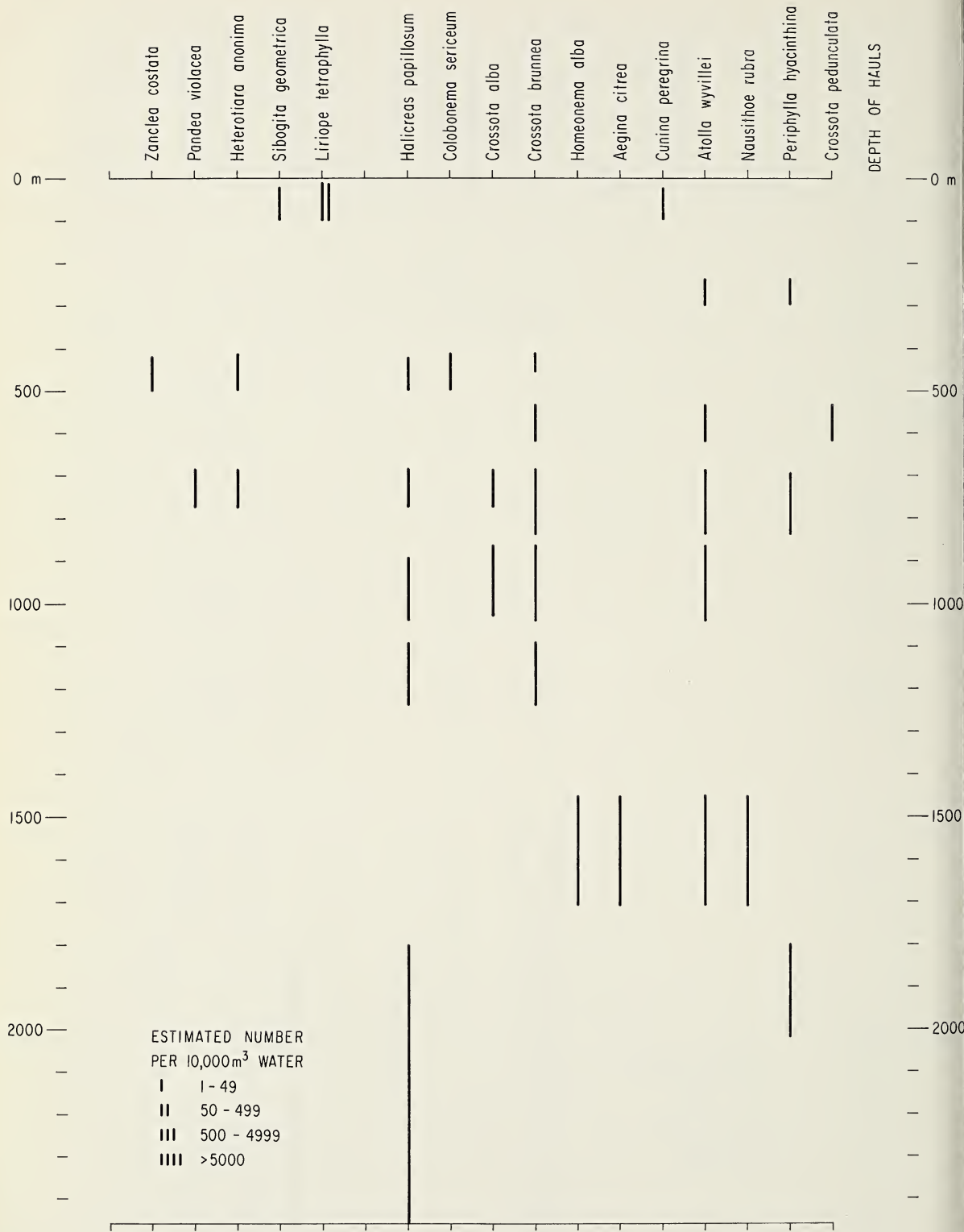
FIG. 6.   Bathymetric distribution of Medusae during the night series.

Halicreas papillosum 30 mm in diameter were present at 775–685 m, and those 50 mm in diameter at 1242–1090 m. Specimens of *Periphylla hyacinthina* up to 25 mm high appeared at 300–235 m, whereas at 840–690 m they were 35 mm high. *Colobonema sericeum* up to 40 mm in height were found at 460–410 m, and below this level those 50 mm in height.

CTENOPHORAE

Beroe spp. extended in the night series from 10 m (uppermost sampling) to 500 m, and during daylight from 0 to 525 m.

CONCLUSIONS ON BATHYMETRIC DISTRIBUTION

Several striking features were observed in the bathymetric distribution:

1. The number of species of Chaetognatha and Siphonophorae in the upper 100 m was higher during daylight than at night.

2. The number of specimens for the species of Chaetognatha present both in daylight and at night in the upper 100 m was either of the same numerical magnitude or, in most cases, higher at night.

3. In general, the difference in the number of specimens observed in the right and left net for the upper 100 m was greater during daylight than at night.

Points 1 and 3 suggest either that during daylight the patches of specimens are denser, or that at night the individuals are scattered throughout a bigger region, thus providing fewer individuals per cubic unit of water. This conclusion appears to be in contradiction with established statements, which maintain that planktonic organisms congregate more at night than in daylight. Another possibility is that they can avoid the net better in daylight than at night. The sky condition at night, when the hauls were taken, was one of darkness, without moonlight; but there are no data on bioluminiscence.

Therefore, these preliminary studies appear to indicate that individuals are not evenly distributed, but that there is a small pattern of patchiness included in the total region populated by certain species. By using the paired net it will be possible to detect either this patchiness within the distributional region of the species, or the flocking of individuals when disturbed (a general behavior response observed in nature).

DISTRIBUTION OF THE ORGANISMS AND THE POSITION OF THE SCATTERING LAYER

Unfortunately, samplings were not made at depths at which the scattering records appeared. However, they could be determined easily by correlating records and samples taken at the same time and date. For example, at 1238–

TABLE 1
SPECIES IN THE UPPER 110 M CORRELATED WITH THE SHALLOWER SCATTERING (DAYLIGHT)

| GROUP | CONCENTRATION OF INDIVIDUALS PER 10,000 M³ OF WATER FILTERED | | | |
	GREATER THAN 5,000	4999–500	499–50	LESS THAN 50
Chaetognatha	S. bierii	S. minima S. pseudoserratodentata	K. subtilis S. bipunctata S. decipiens S. enflata S. euneritica	P. draco S. hexaptera S. pacifica S. scrippsae
Siphonophorae			M. atlantica E. russelli Ch. appendiculata N. reticulata	E. spiralis L. subtiloides A. acaule St. bijuga
Medusae		L. tetraphylla		P. discoidum C. alba
Ctenophorae				Beroe spp.

TABLE 2

SPECIES IN THE 350–250 M LAYER, PARTIALLY COINCIDENT WITH THE
DEEPEST SCATTERING RECORD (DAYLIGHT)

	CONCENTRATION OF INDIVIDUALS PER 10,000 M³ OF WATER FILTERED			
GROUP	GREATER THAN 5,000	4999–500	499–50	LESS THAN 50
Chaetognatha	S. bierii S. decipiens	S. scrippsae	S. maxima	K. subtilis S. bipunctata S. euneritica S. hexaptera S. minima S. pacifica S. zetesios
Siphonophorae				Ch. appendiculata L. multicristata L. conoidea N. dubia St. rubra Ph. hydrostatica B. elongata
Medusae				S. coccometra L. tetraphylla C. alba C. brunnea

1550 hours on 5 September 1965, bright and sunny with calm sea, scattering layers appeared at 91 m, 200 m, and 345 m. The species observed coincidently are detailed in Tables 1 and 2.

The nighttime scattering layer at 2038–2345 hours on 3 September 1965 appeared to be 54.60 m thick at the upper levels, and at a depth of 218.40 m it was 36.40 m thick. The species observed coincidently are detailed in Tables 3 and 4.

The siphonophores considered to be most probably responsible for the production of scattering are the Physonectae, those with floats containing gas (CO). Species of that group (*Stephanomia bijuga, St. rubra,* and *Physo-*

TABLE 3

SPECIES IN THE 100–20 M LAYER, PARTIALLY COINCIDENT WITH THE
SHALLOWER SCATTERING RECORD (NIGHT)

	CONCENTRATION OF INDIVIDUALS PER 10,000 M³ OF WATER FILTERED			
GROUP	GREATER THAN 5,000	4999–500	499–50	LESS THAN 50
Chaetognatha		S. bierii	S. euneritica S. hexaptera	P. draco S. enflata S. minima S. pseudoserra-todentata
Siphonophorae			M. atlantica E. spiralis Ch. appendiculata	A. ernesti N. reticulata
Medusae			L. tetraphylla	S. geometrica C. peregrina
Ctenophorae				Beroe spp.

TABLE 4

SPECIES IN THE 300–235 M LAYER, COINCIDENT WITH THE DEEPEST SCATTERING RECORD (NIGHT)

GROUP	GREATER THAN 5,000	4999–500	499–50	LESS THAN 50
		CONCENTRATION OF INDIVIDUALS PER 10,000 M^3 OF WATER FILTERED		
Chaetognatha		S. decipiens	S. bierii S. hexaptera S. scrippsae	K. subtilis S. enflata S. maxima S. zetesios
Siphonophorae			M. atlantica L. conoidea	Ch. appendiculata L. achilles L. havock L. multicristata St. bijuga B. elongata A. ernesti R. plicata
Medusae				A. wyvillei P. hyacinthina
Ctenophorae				Beroe spp.

phora hydrostatica) were observed at the levels of scattering. It is also probable that the head armature (hooks, teeth, and chitinous plates) of the chaetognaths will contribute to scattering.

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Ecological Significance of a Drifting Object to Pelagic Fishes

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Pelagic fishes frequently gather around drifting material in the open sea. Commercial and sport fishermen regard the immediate vicinity of drifting material as a potentially good area for trolling. Commercial seine and pole-and-line fishermen in Japan, Indonesia, and Malta anchor floating material to attract fish. Fish have been reported gathered around floating algae, coconuts, and pumice (Besednov, 1960; Senta, 1965); floating logs (Inoue, Amano, and Iwasaki, 1963; Kimura, 1954; Yabe and Mori, 1950); coconut fronds and slabs of cork (Hardenberg, 1949; Soemarto, 1960; Galea, 1961); and rafts (Kojima, 1960; Heyerdahl, 1950; Evans, 1955). In addition to clustering near these inanimate objects, the young of many pelagic fishes gather beneath jellyfish (Mansueti, 1963); fish-jellyfish associations have much in common with the associations studied in the present paper.

Hypotheses suggested to explain the accumulation of fish around inanimate floating objects include: (1) fish seek shelter from predators (Soemarto, 1960; Suyehiro, 1952); (2) larger fish prey on the concentration of smaller fish (Kojima, 1956); (3) fish feed on algae or decaying coconut fronds (Reuter, 1938; Soemarto, 1960); (4) fish seek the shade under the object (Suyehiro, 1952); (5) fish use floating objects as a substrate on which to lay their eggs (Besednov, 1960); (6) the shadow of the object makes zooplankton more visible to the fish (Damant, 1921). At the beginning of the present study we suggested still another hypothesis: floating objects are cleaning stations, where pelagic fishes have their parasites removed by other fish. Such symbiotic cleaning associations are well documented for fishes in inshore waters (Eibl-Eibesfeldt, 1955; Limbaugh, 1955, 1961; Randall, 1958).

To test these hypotheses, studies were made from a raft with an observation chamber (Fig. 1) built at the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, and set adrift in the central Pacific (Gooding, 1965). The present paper describes and interprets the observations in light of the above hypotheses.

AREAS AND METHODS OF OBSERVATION

Observations were made in two areas, one off the leeward coast of the island of Hawaii and the other near the Equator in the central Pacific (Fig. 2).

Observations were made in Hawaii between September 28 and October 11, 1962, and between August 1 and August 26, 1965. This area offers two advantages: first, it is sheltered from the northeast trade winds and the sea is relatively calm; second, essentially pelagic conditions (water deeper than 800 m) occur within 1 mile of shore. During 345 hours of drift, 173 hours of daylight observations and 9 hours of night observations were recorded. Eleven drifts were made, the longest of which was 52 hours.

Two drifts were made between February 14 and March 20, 1964 in the storm-free belt at the convergence of the northeast and southeast trade winds near the Equator. On the first drift the raft was launched 9 nautical miles north of the Equator in an area of upwelling. During 194 hours of drift, 91 hours of daylight observations were made. The second equatorial drift began 153 nautical miles south of the Equator. During 215 hours of drift, 100 hours of daylight observations were made.

The raft drifted 585 nautical miles west during the first equatorial drift and 395 nautical miles west during the second. Most of the drift was due to surface currents. To reduce wind-induced drift a 28-foot parachute was used as a sea anchor during part of the first drift and all of the second. (It was also used during several of the Hawaiian drifts.)

While the raft was adrift, wave heights ranged from 0 to 1 m at Hawaii and from 1 to
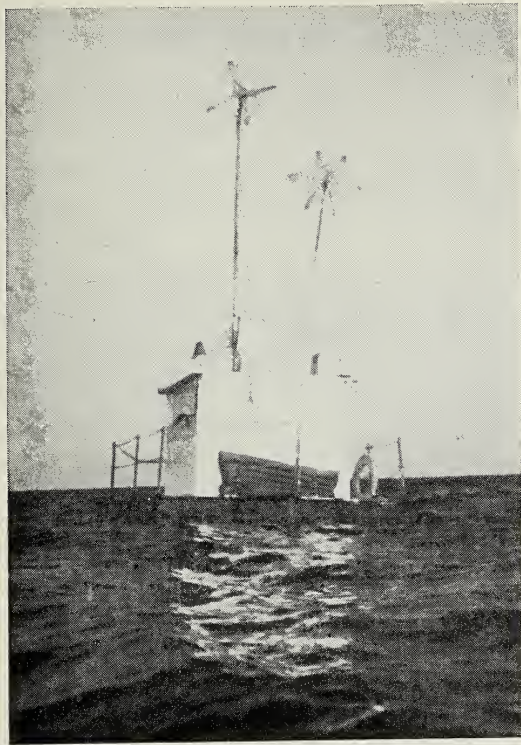
FIG. 1. The observation raft used in study.

FIG. 2. Areas in which drifts were made with the observation raft, off Hawaii (*upper panel*) and near the Equator (*lower panel*).

2 m at the Equator. Average wind speeds ranged from 10 to 15 knots. Cloud cover seldom exceeded 30%.

The observation chamber beneath the raft (Fig. 3) accommodated a single observer, who could view the area beneath and around the raft. Two observers manned the drifting raft from dawn to dusk. Watch positions in the chamber were rotated each hour. Nights were spent on the ship, which remained 1–3 miles from the raft. A skiff provided transportation between ship and raft.

The observers noted the number of each kind of fish at the raft, their position under or near the raft, and their reaction to the raft and to other fish or invertebrates. Night observations were made under bright moonlight, but a flashlight was used at intervals to determine more accurately the positions of the fish. The accumulation was quantified by making population counts of the species present at intervals during the day. An estimate of population changes during the night was obtained by comparing the last count in the evening with the first count on the following morning.

FIG. 3. The observation chamber of the raft. Dark specks to right of chamber are small fish. The white object behind the chamber is the parachute drogue.

In addition to direct observations, 6,200 ft of 16-mm color movies, and numerous still pictures were taken.

Fish were captured at the raft with dip nets, baited hooks on hand lines, casting and trolling lures, and a small purse seine net attached to the sides of the raft. To avoid interference with the accumulation of animals, collections were made only at the end of the drifts. Stomach contents and external parasites of fish captured at the raft were preserved.

FISHES AT THE RAFT

Animals seen from the observation chamber (some are shown, as photographed from the chamber, in Figures 4a–f) were broadly
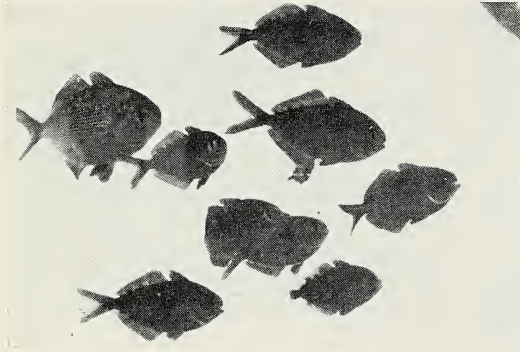
FIG. 4a. Freckled driftfish.
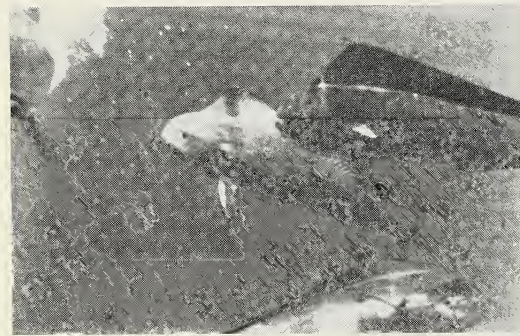
FIG. 4b. Adult dolphin.
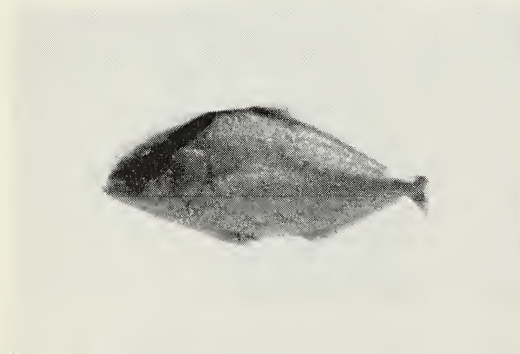
FIG. 4c. Amberjack.
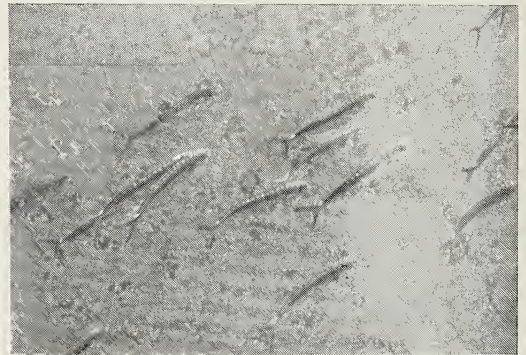
FIG. 4d. Juvenile dolphin.

FIG. 4e. Whitetip shark accompanied by pilotfish and remora.
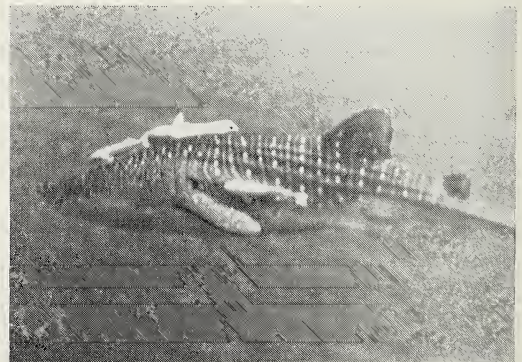
FIG. 4f. Whale shark accompanied by remora.

grouped as transients, visitors, or residents (Table 1) on the basis of their reaction to the raft and the length of time they remained near it. Transients (many of which were flyingfish, Exocoetidae) did not appear to react to the raft, but were usually visible only momentarily as they swam by. Visitors did not aggregate at the raft, but appeared to react to it; they usually remained near it for several minutes to an hour. Residents aggregated at the raft; some stayed in view more or less permanently, and others swam out of view for several hours but usually returned. Different individuals of certain species did not always react in the same way to the raft; these species were consequently placed in more than one category.

Residents were of two types: smaller fishes which stayed in the immediate vicinity of the raft and were usually in view of the observer; and large carnivores that were frequently out of view for several hours. When reappearing after a prolonged absence, the individual or group could often be identified by distinguishing characteristics such as abrasions, parasites, scars, the number in the group, and body size. The relation of all resident species to the raft was facultative, since each also occurs independently of any association with drifting objects.

Small resident fishes were: freckled driftfish, *Psenes cyanophrys* (Cuvier); juvenile pilotfish, *Naucrates ductor* (Linnaeus); rough triggerfish, *Canthidermis maculatus* (Bloch); scrawled filefish, *Alutera scripta* (Osbeck) (but only individuals exceeding about 20 cm, smaller ones behaving as visitors); amberjack, *Seriola rivoliana* Cuvier and Valenciennes; juvenile greater amberjack, *Seriola dumerili* (Risso); juvenile jack, *Caranx* sp.; adult and juvenile mackerel scad, *Decapterus pinnulatus* (Eydoux and Souleyet); juvenile skipjack tuna, *Katsuwonus pelamis* (Linnaeus); juvenile yellowfin tuna, *Thunnus albacares* (Bonnaterre); juvenile dolphin, *Coryphaena* sp.; and juvenile stages of four reef fishes—damselfish, *Abudefduf abdominalis* (Quoy and Gaimard); sea chub, *Kyphosus cinerascens* (Forskål); goatfish, *Mulloidichthys samoensis* Gunther; and squirrelfish, Holocentridae.

The large predatory residents were: dolphin, *Coryphaena hippurus* Linnaeus; wahoo, *Acanthocybium solandri* (Cuvier); rainbow runner,

Elagatis bipinnulatus (Quoy and Gaimard) and whitetip shark, *Carcharhinus longimanus*, usually accompanied by adult pilotfish and remoras, *Remora remora* (Linnaeus).

The freckled driftfish was by far the most common resident in both drift areas. On all drifts it was the first to appear, had the highest rate of accumulation (Table 2), and attained the largest population. At the end of the second equatorial drift, 729 were caught in the purse seine and several hundred escaped. Many were also caught at the end of other drifts. Freckled driftfish usually came to the raft singly or in small groups. Once a green turtle, *Chelonia mydas*, came to the raft accompanied by nine driftfish and one remora. The turtle left with the remora after a few minutes, but the driftfish remained with the raft.

Residents accumulated more rapidly by day than by night. Statistics on the average rate of accumulation of some of the more common residents appear in Table 2. Less common residents, not listed in Table 2, also accumulated more rapidly by day than by night.

Species composition differed between the Hawaiian and equatorial areas. Only 38% of the 27 fish identified to species in Table 1 were seen in both areas. Three of the more common species off Hawaii, the rough triggerfish, dolphin, and damselfish, were either absent or rare in the equatorial waters. Of species that were residents at some stage in their life history, 62% were common to both areas, whereas none listed only as a visitor was common to both areas. Some of the apparent differences between the areas could have resulted from differences in the time of year or could even be attributable to the sample sizes. For example, the occurrence of rainbow runners, pompano dolphin (*Coryphaena equiselis* Linnaeus), and green turtles in the equatorial but not the Hawaiian area may well be irrelevant, for all are common in Hawaiian waters.

ADAPTIVE SIGNIFICANCE

Our observations provided relevant information on the hypotheses that floating material (1) provides protection from predators, (2) concentrates the food supply, and (3) acts as a cleaning station. These hypotheses, of course,

TABLE 1

Animals Seen from the Observation Chamber of a Drifting Raft*

SPECIES, GENUS, OR FAMILY (Common Name in Parentheses)	DRIFT LOCATION	BEHAVIOR CATEGORY	FORK LENGTH (cm)	MAXIMUM NUMBER SEEN AT ONE TIME
Abudefduf abdominalis (damselfish)	H	R	$0.7–1.0^†$	24
Acanthocybium solandri (wahoo)	H03	R	45–90	3
Alutera scripta (scrawled filefish)	H	RV	10–35	2
Canthidermis maculatus (rough triggerfish)	H	R	$25–35^†$	33
Caranx kalla (golden jack)	H	V	30	1
Caranx sp. (jack)	H	R	$2.9–5.3^†$	3
Carcharhinus longimanus (whitetip shark)	H03	RV	125–175	2
Chelonia mydas (green turtle)	0	V	60	1
Coryphaena equiselis (pompano dolphin)	03	V	30	100+
Coryphaena hippurus (dolphin)	H03	R	$60–100^†$	70+
Coryphaena sp.	H03	R	10–15	80
Decapterus pinnulatus adult (mackerel scad)	H03	RT	20–25	1,000+
juvenile	3	R	$13.1^†$	1
Diodontidae (spiny puffer)	0	V	12	1
Echeneidae (free-swimming) (remora)	3	R	8	1
Elagatis bipinnulatus (rainbow runner)	3	R	75	1
Exocoetidae (flyingfish)	H03	T	10–15	10+
Fistularia petimba (cornetfish)	H	V	20–40	2
Globicephala scammoni (pilot whale)	H0	V	375	2
Holocentridae (squirrelfish)	H	R	2	1
Istiophoridae (marlin)	H	T	125	1
Katsuwonus pelamis adult (skipjack tuna)	H3	T	45	1,000+
juvenile	3	RV	10–15	50
Kyphosus cinerascens (sea chub)	H	R	$2.5^†$	13
Manta alfredi (manta ray)	H	V	$100–125^‡$	1
Manta sp.	0	V		1

TABLE 1 (*continued*)

SPECIES, GENUS, OR FAMILY (Common Name in Parentheses)	DRIFT LOCATION	BEHAVIOR CATEGORY	FORK LENGTH (cm)	MAXIMUM NUMBER SEEN AT ONE TIME
Mulloidichthys samoensis (goatfish)	H	RV	10–12	1,000+
Naucrates ductor adult (pilotfish)	H03	RV	15–30	7
juvenile	H03	R	2.6–6.7[†]	7
Nomeus gronowi (man-of-war fish)	0	V	2	1
Prionace glauca (great blue shark)	0	V	150	1
Psenes cyanophrys (freckled driftfish)	H03	R	1.5–12.4[†]	1,000+
Remora remora (attached) (remora)	H03	RV	15–30	—
Rhincodon typus (whale shark)	3	V	300	1
Seriola rivoliana[§] (amberjack)	H	R	20[†]	1
Seriola dumerili (greater amberjack)	H	R	3.7	1
Sphyraena barracuda (great barracuda)	H	V	50	1
Thunnus albacares (yellowfin tuna)	H3	RV	25–40	37
Tursiops sp. (bottlenose dolphin)	H0	V	150–200	20+

* Drift Location: H = Hawaii; 0 = 0° Latitude; 3 = 3° S.
  Behavior Category: R = Resident; V = Visitor; T = Transient.
† Measured length; all other lengths are estimated.
‡ Breadth.
§ The first record for Hawaiian waters, identified by Dr. Frank J. Mather, Woods Hole Oceanographic Institution, from a specimen preserved after capture at the raft.

TABLE 2

AVERAGE NET INCREASE OR DECREASE IN NUMBER OF RESIDENTS* AT THE RAFT PER 12-HOUR DAY
AND 12-HOUR NIGHT[†] IN THREE DRIFT AREAS
(Number of 12-Hour Periods in Parentheses)

FISH	HAWAII OCTOBER 1962		HAWAII AUGUST 1965		0° LATITUDE FEBRUARY 1964		3° S MARCH 1964	
	Day (9)	Night (7)	Day (8.5)	Night (4)	Day (7.5)	Night (9)	Day (8.5)	Night (9.0)
Psenes cyanophrys[‡]	24	1	107	1	18	1	100	0
Coryphaena sp. (juvenile)	–	–	–	–	11	–2	1	–1
Canthidermis maculatus	7	2	3	1	–	–	–	–
Coryphaena hippurus (adult)	4	1	10	0	–	–	–	–
Abudefduf abdominalis (juvenile)	4	–1	–	–	–	–	–	–
Decapterus pinnulatus (adult)	–	–	10	–5	2	0	3	–3
Katsuwonus pelamis (juvenile)	–	–	–	–	–	–	3	–3
Naucrates ductor (juvenile)	–	–	–	–	1	–1	–	–

* Only the residents with an average accumulation equal to or greater than one fish per 12 hours of daylight are included.
† Population changes during the night were estimated by comparing the last count in the evening with the first count the following morning.
‡ Increases are based on the rate for the first 100 to gather because larger numbers could not be counted accurately.

are not mutually exclusive. The observations provided less information about the other hypotheses mentioned earlier. All the above hypotheses consider the adaptive significance of floating material in the ecology of pelagic fishes. The stimuli that release the approach of fishes to the raft are not discussed.

Protection from Predation

At least nine species of fish, both large and small, reacted to the raft in a way that made them less vulnerable to predation. Typically, when a predator approached the raft, the prey formed a compact group very close to the understructure. When the predator left or ceased harassments, the prey again dispersed about the raft. Often the predator chased the prey to the raft. The value of the raft to the prey was demonstrated by the fact that only one species, the amberjack, frequently caught fishes that had taken shelter under the raft. Observations on individual prey species are described below.

The most common resident, the freckled driftfish, usually took a position far below and downwind from the raft and was sometimes out of view. Driftfish were able to match their background. They had a silvery countershaded coloration when not under the raft, but took on a mottled brown coloration when close under it, and those collected from under an orange drogue buoy had an orange color. Most of their predator-avoidance activity was in response to dolphins, although some was in response to pompano dolphins, wahoos, bottlenose dolphins (*Tursiops* sp.), or to pilotfish which approached the raft swimming with a whitetip shark. The hundreds of such responses followed an unvarying sequence: when one of the predators came into the vicinity, the freckled driftfish suddenly formed a compact school and swam rapidly back to the raft or the parachute drogue. (They also fled to the raft when an observer entered the water.) When an amberjack was preying upon them, they remained within about 20 cm of the viewing chamber. They attempted to stay on the opposite side of the chamber from the amberjack or dodged into the gaps between the frames of the viewing windows. When the amberjack was not actively feeding, the driftfish ranged out again. Small damselfish,

pilotfish, greater amberjacks, and jacks behaved similarly to driftfish in response to predation, but did not change coloration.

Rough triggerfish ranged far from the raft, sometimes out of sight. Their rapid return to it usually heralded the appearance of a predator (billfish, a great barracuda, bottlenose dolphin, whitetip shark) or apparent predators (schools of mackerel scad or a powerboat). They resumed ranging before the potential predator departed, except when the predator was a bottlenose dolphin. None of the above species exhibited a predatory response towards rough triggerfish. The triggerfish did not return to the raft when manta rays appeared and they usually swam out and met approaching dolphins. Rough triggerfish and dolphins may often be associated in the absence of drifting material; sometimes they arrived simultaneously at the raft.

On several occasions, the most successful piscivore, the amberjack, itself became the potential prey of dolphins and took shelter beneath the raft. Although amberjacks frequently ranged 10 to 15 m from the raft unmolested, when the dolphin began pursuit the amberjack eluded the predator by swimming close to the chamber. It remained there for some time before ranging out again.

The dolphin, one of the largest residents, took shelter close under the raft three times: once in response to a bottlenose dolphin, once to a billfish, and once to a swimmer. Each time the dolphin swam around the chamber just under the flotation drums and took on a coloration (Fig. 5) that occurred in no other situation

Fig. 5. The lower dolphin assumed the dark coloration when one of the observers entered the water.

and had not previously been recorded (for other colorations of this species, see Murchison and Magnuson, 1966). The dorsal half of the body turned a dark brownish-black. A sharp separation extended longitudinally along the side between the dark dorsal area and the silvery ventral half of the body. The above behavior and coloration, observed only when 1 or 2 dolphins were at the raft, were different from those seen on similar occasions when 13 or more dolphins were present. Then the group of dolphins swam immediately behind a billfish, a whitetip shark, bottlenose dolphin, and a swimmer near the raft. A position immediately behind a potential predator may be of advantage to the prey provided the animal has the speed and maneuverability to maintain such a position.

Large schools of goatfish attempted to avoid dolphins and amberjacks by swimming to the other side of the raft, but only rarely did individuals use the maximum shelter of the raft by swimming under it. As a consequence both predators were able to prey upon them successfully.

One of the most clearcut examples of predator avoidance occurred when a golden jack was chased to the raft by the feeding attacks of five dolphins. The dolphins stopped their feeding passes after the jack swam under the raft. For several hours the jack swam within inches of the chamber. The observer on deck could reach into the water and touch the fish without driving it away. After several hours it began to swim under the flotation drums, but not away from the raft. About 8 hours after it arrived the jack joined a whitetip shark and six pilotfish which swam close by, and left the raft in their company. The dolphins took on their feeding coloration, but did not attack the jack as it swam off with the shark. This incident provided evidence for the protective role that both floating objects and large animals such as sharks play for the fish that accompany them.

Concentration of Food Supply

It has often been said that floating material concentrates the food supply—smaller fish, zooplankton, or sessile biota. Most piscivores did not successfully prey on fish that sought shelter beneath the raft, but they did prey extensively on those that gathered at the raft but did not take shelter beneath it. Zooplankton was not concentrated at the raft, nor did large numbers of sessile organisms attach themselves to it.

Kojima (1956) suggested that dolphins were found near floating objects because more food was available there, but was unable to demonstrate that they fed substantially on other fishes gathered at anchored bamboo rafts (Kojima, 1960, 1961). Yabe and Mori (1950) argued that abundance of food was an inadequate explanation for the presence of yellowfin and skipjack tuna near floating logs because the fish took bait readily and did not have much food in their stomachs. The simultaneous presence of piscivores and potential prey near the raft was well documented, yet, as mentioned above, only amberjack successfully preyed on the small fish that took shelter there. We saw them chase and eat freckled driftfish. The stomach of the only amberjack taken at the raft contained three driftfish. The only other species we saw catch smaller fish was the adult dolphin. Both it and the amberjack, as has been mentioned, preyed on schools of goatfish that were near the raft, but not under it. The stomachs of 53 dolphins caught near the raft contained only 5 scrawled filefish; 1 sargassum triggerfish, *Xanthichthys ringens* (Linnaeus); and 1 puffer, *Diodon holocanthus* Linnaeus. All were juveniles. Once we saw an adult dolphin seize and eat a freckled driftfish which was attempting to reach the raft. This incident suggests that dolphins sometimes intercepted driftfish seeking shelter. Possible supporting evidence for this supposition came from observations off Hawaii. While the raft was anchored for several days, numerous freckled driftfish, 19 dolphins, and 1 amberjack accumulated. The raft was then towed by the ship 30 miles down the coast and set adrift. During the tow the driftfish were outdistanced and all were lost; only the dolphins and amberjack remained. Thus, unlike other drifts, this drift began with a number of fish—19 dolphins and 1 amberjack—at the raft. During 52 hours of drifting no freckled driftfish appeared. Yet in the same area, two weeks earlier, approximately 500 and 200 driftfish gathered at the raft on two drifts of 50 and 32 hours, during which only 2 and 7 dolphins had accumulated.

Two other predators, wahoos and adult pilot-fish (with sharks), actively chased smaller fishes at the raft, but were not observed to catch any.

Although zooplankton was not concentrated at the raft, a number of fishes that eat zooplankton gathered there. For example, stomachs of 10 rough triggerfish caught at the raft contained many pteropods and stomatopods, and lesser numbers of crab megalops and zoea, amphipods, and copepods. Stomachs of 81 freckled driftfish contained small pelagic tunicates (*Oikopleura* sp.), copepods, fish eggs, chaetognaths, and various coelenterates. These fish also bit at macroplankton such as ctenophores and tunicate colonies. Stomachs of 24 damselfish contained only *Oikopleura* sp. Stomachs of nine small pilotfish contained mostly copepods. All of these fishes, and also scrawled filefish and goatfish, frequently darted after and caught zooplankton around the raft. The wind slowly pushed the raft through the water at a speed faster than the swimming speed of the small zooplankters. Thus, there was no accumulation of zooplankton, but rather a continuous stream of macroplankton and microplankton slowly moving past the underwater windows.

Finally, fishes at the raft did not feed on the small amounts of sessile or ambulating biota present. Only the rough triggerfish bit at the raft. Crab megalops occasionally settled on the underside of the raft or on the triggerfish, but those in the stomachs could have been taken as well from the plankton as from the raft. Perhaps a greater growth of biota on the raft would have altered the feeding behavior, especially of the triggerfish, which has a dentition suited for grazing. Evans (1955) reported that triggerfishes (*Balistes* sp., and *Canthidermis* sp.) cropped barnacles fringing the waterline of a drifting vessel in the Atlantic North Equatorial Current.

Removal of Ectoparasites

At the beginning of this study we hypothesized that floating objects serve as cleaning stations where fishes may gather to have parasites removed by other fish. Many fish observed at the raft carried ectoparasites, and several events suggested that these were eaten by other fish. Fish also chafed against the raft, another possible aspect of cleaning behavior.

Small copepods were found on captured dolphins, freckled driftfish, and rough triggerfish, and were seen on whitetip sharks and juvenile dolphins (*Coryphaena* sp.). Crab megalops and parasitic isopods were also seen on triggerfish. The megalops walked freely over the fish; the isopods were firmly attached.

Biting behavior was common among rough triggerfish and was directed toward a triggerfish that was headstanding (body oriented head down), apparently soliciting predation on parasites. This behavior occurred only when more than one triggerfish was present; it was common 3 to 12 m from the raft. The headstanding fish did not flee the biting fish and once even appeared to rotate its body, keeping the side with the parasitic isopod toward the biting fish. The biting was always directed at the headstanding fish even though several other fish were very close by. Although we did not witness directly the removal of a parasite, we saw one rough triggerfish bite at a parasitic isopod on the caudal peduncle of another, and soon afterward the isopod was missing. Biting did not appear to represent aggressive behavior; intraspecific aggression among triggerfish frequently occurred immediately under the raft, but did not include headstanding. In aggression one triggerfish repeatedly chased others from under the raft.

Once a rough triggerfish swam to a dolphin and apparently nipped at it. The dolphin, some distance from the raft, had begun leaning to one side. It had also stopped swimming and was almost motionless in the water. It leaned four times within 2 minutes, for periods of about 9 seconds. Similar leaning behavior by dolphins in the presence of rough triggerfish was seen on several other occasions, but did not elicit nipping by the latter. This behavior was not unlike that of inshore fishes soliciting parasite-cleaning labrids (Randall, 1958). Balistids are not among the reported inshore parasite-pickers, but their dentition should make them efficient in this role.

A juvenile dolphin, *Coryphaena* sp., with a small reddish copepod attached near the fork of the caudal fin repeatedly positioned itself so that its caudal fin was close to the head of

FIG. 6. Adult dolphin chafing against a 55-gallon drum beneath the raft.

another juvenile dolphin, *Coryphaena* sp. During the display the fish with the ectoparasite stopped caudal movements and treaded water with its pectorals. It did not lean to one side as did the adult dolphin mentioned above. On numerous occasions, the juvenile dolphin, *Coryphaena* sp., to which the display was directed made passes at the caudal fin of the parasitized fish. At the end of the day, however, the copepod was still attached.

Several species chafed their sides on the raft, skiff, or lines hanging in the water. Adult dolphin commonly chafed against the bottom of the raft and skiff (Fig. 6). Sanchez Roig and Gomez de la Maza (1952) and Heyerdahl (1950) have reported similar behavior. Sometimes dolphin chafe against other fish (Breder, 1949). In one of our film sequences, a small abrasion can be seen on the side that the fish was rubbing against the skiff. Other species at the raft which were seen chafing were rough triggerfish on the bottom of the raft; juvenile dolphin on ropes and on the caudal and dorsal fins of whitetip shark; whale shark, whitetip shark, and scrawled filefish on the rope to the parachute drogue; and a spiny puffer, on a small floating can. This behavior, especially common in the coryphaenids, could remove parasites or relieve skin irritation.

Some predation on ectoparasites occurred at the raft, but the question remains whether the removal of parasites is concentrated near the raft and other floating objects. It is obvious that removal of parasites by chafing on hard objects would be concentrated near floating material or larger fishes. In addition, the opportunity to feed on ectoparasites or to solicit parasite cleaning would appear to be greater near the raft because the fishes usually arrived in small groups or alone and formed larger aggregations at the raft.

Other Possible Explanations

The hypothesis that fishes seek shade under floating objects has no substance. Yabe and Mori (1950) and Kojima (1956) also reached this conclusion. None of the smaller species tended to remain in the shade of the raft. Larger species such as rough triggerfish, wahoo, dolphin, and whitetip shark often ranged far from the raft and were seldom in its shadow. The hypothesis (Besednov, 1960) that fish use floating material as a substance on which to lay their eggs could not be substantiated. Even though fish eggs are frequently found on drifting material, no fish deposited eggs on the raft nor were any eggs seen on the undersurface. No data were obtained to test the hypothesis (Damant, 1921) that the shadow of an object makes the zooplankton more visible to fish. Four species fed upon zooplankton; the visibility of these zooplankters may have been increased by the raft's shadow.

CONCLUSION

A floating object in the pelagic environment provides a relatively rare "superstrate" in an environment notable for its horizontal homogeneity. This superstrate has some of the same ecological significance to certain pelagic fishes that a substrate has to inshore fishes. Obviously, no single biological association or adaptive advantage can explain the occurrence of fish around floating objects at sea. Of the ecological hypotheses considered, shelter from predation is substantiated best and appears to be the most significant factor in the evolution of fish communities that gather beneath inanimate drifting material in the open ocean.

graphic Institution, who verified the new record for Hawaii of *Seriola rivoliana;* John E. Randall, The Oceanic Institute and the Bishop Museum, Honolulu, Howard E. Winn, University of Rhode. Island, Philip Helfrich, University of Hawaii, Thomas A. Manar, and Donald W. Strasburg, Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Charles M. Breder, Jr., American Museum of Natural History, and John H. Hunter, Bureau of Commercial Fisheries Tuna Resources Laboratory, La Jolla, California, who reviewed the manuscript during various phases of its development.

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A Possible Relation between the Occurrence of a Dendritic Organ and the Distribution of the Plotosidae (Cypriniformes)

W. J. R. Lanzing[1]

ABSTRACT: Three marine species of Plotosidae are found along the coastlines of the Indian and Pacific oceans, but the other 25 species occur exclusively in the Australian region. The majority of the Plotosidae are freshwater inhabitants, some of which are indigenous to both Australia and New Guinea. The marine members of the family and two freshwater members possess a dendritic organ. It is suggested that this organ has an osmoregulatory function.

IN THEIR DESCRIPTION of the catfish *Plotosus anguillaris*, Bloch (1794) and LaCépède (1803) mention the presence of a peculiar external structure situated posterior to the vent and between the pelvic fins. Cuvier and Valenciennes (1840) observed that this structure had no connection with the urogenital system, but was attached to the last abdominal vertebra by means of a long tendon. According to Brock (1887) and Hirota (1895) this so-called dendritic organ consists of numerous well-vascularized epithelial folds. Weber and de Beaufort (1913), Taylor (1964), and Munro (1966) used the presence of this organ as a criterion in their keys to the family Plotosidae. However, apart from its use in taxonomy this structure has attracted very little attention.

Recently, electron microscope studies by van Lennep and Lanzing (1966) have shown that the dendritic organ of *Plotosus anguillaris* (Bloch), *Cnidoglanis macrocephalus* (Val.), and *Euristhmus lepturus* (Gunther) possesses two main cell types: principal cells containing parallel groups of cytoplasmic tubules and many mitochondria, and clear cells containing an unusual three-dimensional network of cytoplasmic tubules. Because of a similarity between these cells and those occurring in salt glands of sharks and marine birds and the chloride cells in fish gills, the authors suggested that the plotosid dendritic organ is involved in salt transport. This assumption has led to a study of a possible relation between the occurrence of a dendritic organ and the distribution of the Plotosidae in marine and freshwater environments.

DISTRIBUTION OF THE SILUROIDEI

The siluroids of the Austral-Asian region are best represented in the area bounded by Thailand, Vietnam, and Indonesia. The following families occur in this region: Akysidae, Amblycipitidae, Bagridae, Chacidae, Clariidae, Heteropneustidae, Plotosidae, Schilbeidae, Siluridae, Sisoridae (Bagariidae), and Tachysuridae (Ariidae). Except for the Tachysuridae and three species of Plotosidae none of these catfish are found east of the line of Wallace. In the Australian region, which includes Australia, New Guinea, and some adjacent islands (Darlington, 1957), only the Doiichthyidae, Plotosidae, and Tachysuridae occur.

DISTRIBUTION OF THE PLOTOSIDAE

All known species of Plotosidae are inhabitants of the Australian region, but three marine species have a much wider range (Fig. 1). *Paraplotosus albilabris* (C. et V.) occurs in Indonesia, Vietnam, and the Philippines (Suvatti, 1950; Herre, 1953; Kuronema, 1961). *Plotosus canius* Ham. Buch. is reported from East Africa as well as from Fiji (Fowler, 1959), but does not seem to occur in China or Japan. On account of its wide range it is surprising that it has not yet been reported from Australia, although it is present in New Guinea (Munro, 1958). *Plotosus anguillaris* (Bloch) is distributed over a vast area. The western
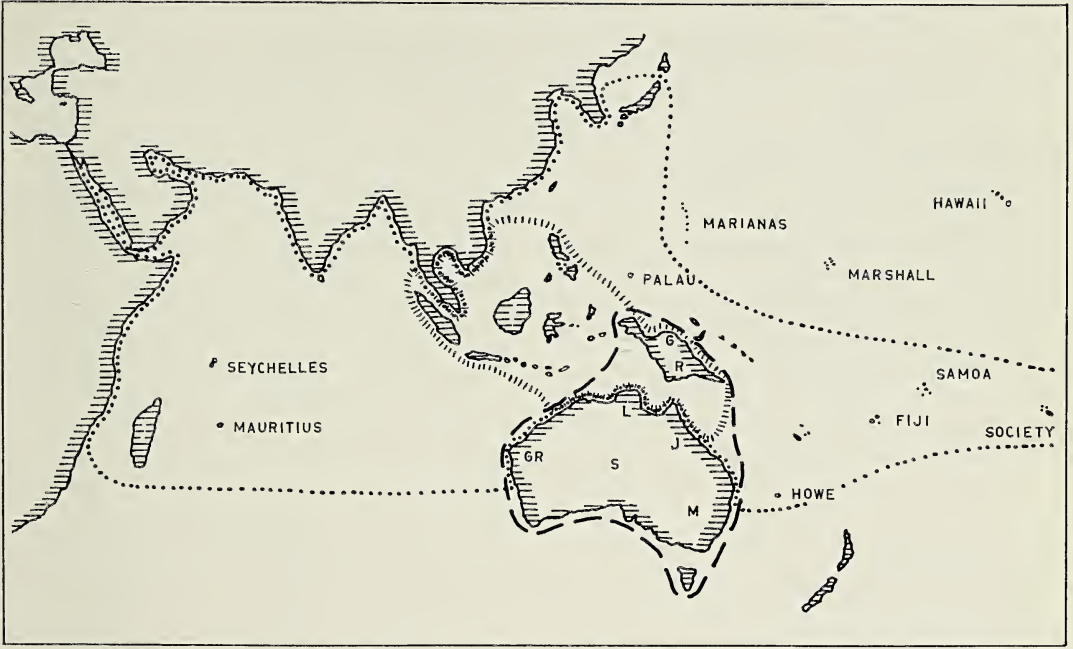
Fig. 1.   Distribution of the Plotosidae. — —, Principal range of the Plotosidae; . . . , range of *Plotosus anguillaris; / / /,* range of *Paraplotosus albilabris.* For letter symbols see footnote for Table 1.

limit of its range is formed by the Southwest Asiatic Barrier (Ekman, 1953), as it has been found in the Red Sea and the Suez canal (Fowler, 1956). Although present along the East African coast, it does not reach Cape Town (Smith, 1949). It occurs in Korea (Mori, 1952) and Japan (Okada, 1955) as well as in the Society Islands; the Eastern Pacific Barrier (Ekman, 1953) apparently forms the eastern limit of its range. *Plotosus anguillaris* is not recorded from the Marshall and Marianas Islands (Schulz, 1953), which ichthyologically are more related to the Hawaiian region.

The distribution of the other plotosids, however, is strictly limited to the Australian region. Of the marine plotosids only *Cnidoglanis macrocephalus* is found all along the coast of mainland Australia, Tasmania, and New Guinea; the other marine species occur only in the northern half of Australia and in New Guinea. Most of the freshwater plotosids are indigenous to the Leichhardtian fluvifaunula (see map by Whitley, 1959), although *Tandanus tandanus* Mitchell, for instance, is confined to the Mitchellian fluvifaunula. Table 1

shows that several freshwater plotosids are common to both Australia and New Guinea (e.g., *Porochilus obbesi* Weber). Other species are exclusively New Guinean, e.g., *Neosilurus gjellerupi* (Weber), or Australian, e.g., *Tandanus tandanus.* Munro (1964) recently drew attention to the existence of differences between the ichthyological fauna of northern New Guinea (Gaimardian fluvifaunula) and that of southern New Guinea (Riechian fluvifaunula). Apparently, some plotosids like *Neosilurus gjellerupi* and *N. ater sepikensis* (Whitley) live in the Gaimardian area, whereas *N. brevidorsalis* (Gunther) and *N. ater ater* (Perugia) are confined to the Riechian area.

THE PRESENCE OF A DENDRITIC ORGAN AMONG THE PLOTOSIDAE

Table 1 lists two groups of Plotosidae: the species in group A possess a dendritic organ, whereas this organ is lacking in the plotosids of group B. The species of group A occupy a marine or estuarine habitat, but thus far *Oloplotosus mariae* Weber and *Plotosus papuensis* Weber have been found only in fresh water

TABLE 1

DISTRIBUTION AND HABITATS OF THE PLOTOSIDAE*

SPECIES	AUSTRALIA	NEW GUINEA	HABITAT
Group A (dendritic organ present)			
1. *Cnidoglanis macrocephalus* (Val.)	+	+	marine
2. *C. microceps* (Rich.)	+	—	marine
3. *C. muelleri* (Klunzer)	+	—	marine
4. *Euristhmus lepturus* (Gunther)	+	+	marine
5. *E. nudiceps* (Gunther)	+	+	marine
6. *Oloplotosus mariae* Weber	—	+ R	fresh water
7. *Paraplotosus albilabris* (Val.)	+	+	marine
8. *Plotosus anguillaris* (Bloch)	+	+	marine
9. *P. canius* Ham. Buch.	—	+	marine
10. *P. papuensis* Weber	—	+ R	fresh water
Group B (no dendritic organ)			
1. *Anodontiglanis dahli* Rendahl	+ L	—	fresh water
2. *Neosilurus argenteus* (Zietz)	+ S	—	fresh water
3. *N. ater ater* (Perugia)	+ L	+ R	fresh water
N. ater sepikensis (Whitley)	—	+ G	fresh water
4. *N. bartoni* Regan	—	+ R	fresh water
5. *N. brevidorsalis* (Gunther)	+ L, J	+ R	fresh water
6. *N. equinus* (Weber)	—	+ R	fresh water
7. *N. gjellerupi* (Weber)	—	+ G	fresh water
8. *N. glencoensis* (Rendahl)	+ L	—	fresh water
9. *N. hyrtlii* Steindachner	+ L, J	—	fresh water
10. *N. idenburgi* (Nichols)	—	+ G	fresh water
11. *N. meraukensis* (Weber)	—	+ R	fresh water
12. *N. mortoni* Whitley	+ L	—	fresh water
13. *N. novaeguineae niger* (Nichols)	—	+ G	fresh water
N. novaeguineae novaeguineae (Weber)	—	+ R	fresh water
14. *N. perugiae* (Ogilby)	—	+ R	fresh water
15. *N. rendahli* (Whitley)	+ L	—	fresh water
16. *Porochilus obbesi* Weber	+ L	+ R	fresh water
17. *Tandanus bostocki* Whitley	+ Gr	—	fresh water
18. *T. tandanus* Mitchell	+ M	—	fresh water

* Symbols used: +, present; —, absent; G, Gaimardian fluvifaunula; Gr, Greyian; J, Jardinian; L, Leichhardtian; M, Mitchellian; R, Riechian; S, Sturtian.

(Weber and de Beaufort, 1913). All the species of group B are freshwater inhabitants.

Examinations carried out on adult and juvenile individuals of *Plotosus anguillaris, Cnidoglanis macrocephalus,* and *Euristhmus lepturus* showed that the dendritic organ is present and equally developed in both sexes, and also that it is already conspicuous in juvenile catfish ranging in size between 45 and 56 mm. Recently, van Lennep (unpublished) found that, in comparison with adults, the dendritic organ of juvenile catfish contains only a relatively small number of fully developed glandular cells.

The mean length of nine adult *Plotosus anguillaris* was 322 mm (286–361 mm) total length. Since some of the gonads were either in a fully mature or in a spent condition, these measurements must represent the size of adult catfish of this species. Comparable figures have been reported by Delsman and Hardenberg (1934), 300 mm; Okada (1955), 250 mm; and Fowler (1959), 460 mm. A much higher figure for maximum size (30 inches) is given by Smith (1949), and is quoted by Munro (1954) and Fowler (1956), but probably is erroneous.

DISCUSSION

More than half of the 28 species of Plotosidae are freshwater inhabitants. This makes

the Plotosidae a predominantly freshwater family rather than a chiefly marine family, as is often implied in the literature (Berg, 1957; Darlington, 1957; Nikolsky, 1961; Sterba, 1963).

It appears that 25 species are found in the Australian region. Three marine species occupy a much larger area covering most of the Indian and West Pacific oceans. Sterba's map (1963) of the distribution of the Plotosidae therefore actually shows the range of one species, namely *Plotosus anguillaris*. It is of interest that among the non-plotosid siluroids only *Tachysurus thallasinus* (Rueppel) has a range as wide as that of *Plotosus canius*, except that the former is also reported from Japan (Matsubara, 1955).

As yet no physiological work has been carried out with regard to the function of the dendritic organ. The available evidence indicates that: (a) its structure resembles that of salt-secreting glands in other vertebrates, (b) it is present in both juvenile and adult plotosids, (c) there exist no sexual differences, and (d) it is not present in freshwater plotosids other than *Oloplotosus mariae* and *Plotosus papuensis*. Hardenberg and Delsman (1934) suggested that the dendritic organ is involved in reproduction, but produced no evidence in support of this claim. A possible respiratory function merits consideration since other catfish (Clariidae, Heteropneustidae) possess accessory respiratory organs. These, however, are in connection with the branchial chambers and are structurally different from the dendritic organ. Furthermore, there seems to be no reason why only marine plotosids should require an accessory respiratory organ. Both marine and freshwater plotosids enter muddy environments that could contain oxygen-deficient water. A salt-excretory function seems to be the most likely, although, admittedly, the presence of a dendritic organ in *Oloplotosus mariae* and *Plotosus papuensis* does not fit in with this theory. Too little is known about these two species to venture any explanation.

According to Darlington (1957:46) marine plotosids may have invaded the Australian region and, after entering a freshwater habitat, reached the end of a complicated line of teleost evolution.

Although evolutionary aspects of zoogeography must remain speculative, it is suggested that the dendritic organ was developed while plotosid ancestors in the Southeast Asian region invaded the sea. This invasion would be different from that of the Tachysuridae, which were able to cope with osmotic stresses by means of mechanisms similar to those used by other old teleost families, such as the Salmonidae. Perhaps because of tachysurid competition, the plotosid ancestors became firmly settled only in the Australian region. From them would have evolved, on the one hand, the freshwater species which lost the dendritic organ in the process. Some of the marine species, on the other hand, managed to disperse radially along the edges of the Indian and West Pacific ocean basins.

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The Family Olividae

John Q. Burch and Rose L. Burch[1]

Shells of the family Olividae are certainly among the most beautiful in form, color, and markings that we possess. Nevertheless, they attract comparatively little attention from the general collector. This is remarkable because the shells are extensively distributed over the globe, are easily collected, and are easily procured at a moderate rate. We believe that this lack of attention is due to the uncertainty with regard to the number of species, and to the lack of reference material. It is difficult to define the limits of many of the species on account of the great variation in color and the extraordinary manner in which the markings gradually change in character while species of other groups are easily distinguished.

Linnaeus (1758) divided the shells we know as the Olividae into 3 species, *Voluta oliva, V. porphyria,* and *V. ispidula.* Gmelin (1791) added a few, and Lamarck (1811), extended the number to 62. Dillwyn (1817) reduced it to 18. Duclos (1835) figured 84 species; he considered that 22 of the species which Lamarck described as distinct were only varieties of other species. Reeve (1850) published figures of 100 species. In 1858 J. E. Gray published "An attempt to distribute the species of *Oliva* into natural groups," but his work did not meet with general acceptance by other authors. In 1870–1871 F. P. Marrat published his "Monograph of the Genus *Oliva*" in which he figured 220 species. In 1883 George W. Tryon published volume V of the Manual of Conchology, which contains his monograph of the Olividae. This was a monumental work, but Tryon was disposed to group related species to a greater extent than most authors have approved. Tryon reduced the number of species to 55. The more recent major publications on this family include those of Johnson (1910–1911, 1915, 1928); Dautzenberg (1927); Dodge (1950); and Olsson and Dance (1966).

Marrat (1870–1871) made the following statement regarding the Olividae: "Specific differences confined within limited areas constitute the exceptions not the rule. In almost every case where the shells can be obtained in numbers they approach the so called species above and below them so as to render it a matter of uncertainty whether they constitute a variety of one or the other." In an effort to trace the relationships between the species Marrat introduced many new names. Sowerby (1870–1871) commented in Thesaurus Conchyliorum: "In his study of the affinities he has been led to register and nominally to admit as species many forms which will appear to the readers as they do to the editor quite indistinguishable."

Ford (1953) said of Marrat: "Judged from the number of forms to which he gave names Marrat might be considered a splitter. Later, however, he stated that the 220 species of *Oliva* might, if carefully examined, be reduced to twenty, and the greater part of his own species reduced to varieties."

The Marrat collection of shells of the Olividae was purchased by the Liverpool Museum in 1875 and remains intact and available. The work of the late J. R. le B. Tomlin listing the species and designating the various type specimens was published by Ford (1953). Tomlin's comments are of great value to the worker on this group. Lamarck's types of the Annales du Museum are in Caen. The Duclos collection is in the Geological Society of London. The Lovell Reeve collection of olives was sold at public auction at the Steven's Auction Rooms. A large part of the specimens were purchased by Marrat and incorporated in his collection. The Weinkauff collection is in the museum at Frankfurt, Germany. All of the great collections of Olividae remain intact in large public institutions. The type specimens representing the work of leading scholars from Lamarck to those of the present day remain available to the serious student. These specimens were named and studied in good faith by recognized workers

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who did original investigation, and they have been studied by a host of serious authors who followed them. It is tragic that we are compelled to abandon such solid material and accept references to a series of poorly drawn old wood cuts. Typical of these are some of Röding in the notorious Museum Boltenianum in which, for some, Röding lists as many as four references all to entirely different species, some of them unrecognizable, and the actual shell has been sold as a curio and lost. What the species may have been is known only to God.

We propose to recognize four major divisions in the Olividae with others as subgenera: *Oliva, Olivella, Agaronia,* and *Ancilla.* On shell characters alone the generic distinctions between *Oliva* and *Olivella* are difficult to define. In general, the species of *Oliva* are larger, although there are many exceptions. *Oliva* has no operculum and no epidermis. In general, *Olivella* is distinguished from *Oliva* by the small size of the shell, its more produced spire, and the presence of a thin horny operculum. Nevertheless, some species of *Olivella,* e.g., *Olivella nivea* (Gmelin, 1791), lack an operculum. Anatomical characters must be considered. The animal of *Olivella* is like that of *Oliva,* but the tentacles and eyes are wanting, the foot is shorter, rounded behind, and does not extend beyond the tip of the spire. Species of *Olivella* are best distinguished from *Oliva* by the radulae. In *Oliva* the radular ribbon generally shows but little variation, the differences between species being small. The ribbon of *Oliva* is generally long and narrow, with many rows of teeth (about 100), while the rhachidian teeth are tricuspidate, the basal margin of the ribbon is wide and often yoke-shaped. In *Olivella* the ribbon is short and wide, with fewer rows of teeth (generally less than 50), the rhachidian teeth are multicuspidate, the cusps being small and numerous. While the rhachidian teeth of both *Agaronia* and *Olivancillaria* are tricuspidate, there are small denticles on the sides that are not present in *Oliva.* The rhachidian teeth of both are very similar in this character. The radula of *Ancilla* is somewhat different. The rhachidian teeth are tricuspidate, but there are two strong lateral teeth.

Some species of *Oliva* are a source of confusion, with various authors accepting different names for the same species. These notes are an attempt to indicate our diagnosis of the taxonomy. We have freely adopted the work of many others. It would seem that the only advantage to be gained from the recognition of color forms is to give the references to the writing of authors in which they frequently add substantially to an understanding of the species involved. With few exceptions there are intergrades in and out of all of them. It is our opinion that naming them is somewhat analogous to describing all of the kittens in a litter. We will discuss the better known color forms that have been given names.

In this paper we will discuss the taxonomy of certain species from the Indo-Pacific of the genus *Oliva* Bruguière 1789.

Oliva oliva (Linnaeus 1758), Systema Naturae, ed. 10, p. 729, no. 350; ed. 12, p. 1188, no. 399.

This species has been confused by many authors with *O. ispidula* (Linnaeus 1758). The recent publication by Olsson and Dance (1966) seems to have established the fact that the true *Voluta ispidula* Linnaeus is a fossil species of *Agaronia,* and that the *O. ispidula* of authors is the *Voluta oliva* of Linnaeus. Generations of authors have described and figured this species as *O. ispidula.* The synonymy is extensive. The figures and discussion given by Reeve (1850) are excellent. Tryon (1883) gives a clear description: "White, ash, yellow, brown, chestnut or chocolate colored, without markings, or with nebulous spots, zigzag lines or reticulations, often with a band near the top of the body whorl; columella white; interior chocolate colored. Length 1–1.5 inches." It is impossible to enumerate the shades and patterns of coloring of this species. The chocolate-colored interior is the most characteristic feature. We will mention a few of the described color forms.

algida Vanatta 1915. Nautilus 29:67–72. It is our opinion that this variety is not sufficiently distinct. It was based, with doubt, on a figure of Reeve (1850). Nevertheless, other workers have accepted this as a variety, and Reeve's figure is clear. The shell is a bluish-white with light-brown longitudinal streaks, a yellow-brown lip, and a shorter spire than usual.

A brown and white callus is seen in the posterior corner of the aperture.

candida Lamarck 1811. Ann. Mus. Hist. Nat. 16:322.
It is doubtful if this is a form of *O. oliva.* The figures represent a much shorter and more obese olive than any example of *O. oliva,* and also the interior of the aperture is white. Nevertheless, others have accepted this form. Dodge (1955) lists it as a recognized variety stating: "An albino form with the aperture more orange than brown."

flaveola Duclos 1845. In Chenu 1845.
Duclos has represented under this name four shells of different colors. According to the description, this variety is light or dark, yellow or orange, the others being of unusual pattern. In this form the interior of the aperture is frequently whitish or rose, but we possess a number of specimens in which it is dark brown. The dark coloration of the aperture nearly always permits identification of this species. This form can be regarded as albinistic, with an aperture of light brown to almost white. Dodge (1955) states: "A yellow form with a white aperture."

gratiosa Vanatta 1915. Nautilus 29:71.
This is a doubtful form and we have failed to recognize it. Vanatta's description is brief and without references: "Shell slender, dark brown, spire elevated, columellar callus cream-white." Dodge (1955) states: "A dark brown, slender form with an elevated spire. It is possibly the form which Lamarck called *O. oriola* (1811) although the spire is considerably higher. The columella is cream-white."

jayana Ducros de St. Germain 1857. Revue Critique, p. 68, pl. III, fig. 44a, 44b.
O. jayana, described as a distinct species by Ducros, is only a form of *O. oliva,* very close to *tigridella* Duclos 1835, having a slender body and short spire. Its pattern is formed of very fine lines composing a condensed network of small triangular meshes. Ducros admitted that he considered his species doubtful. Dodge (1955) described *jayana*: "White or flesh colored with fine longitudinal brown lines and two or more less prominent bands of irregular markings."

lacteana Dautzenberg 1927. J. Conchyl. 71: 49. Dautzenberg stated that the external color is entirely white, without pattern, the aperture brown. He also stated that this form has been confused by many authors with *O. candida* Lamarck 1811. Large series in the Burch collection contain specimens that fit the description in every way, but the gradation into other forms is obvious.

longispira Bridgman 1906. Proc. Malacol. Soc. London 7:195.
This form differs from typical *O. oliva* by having a more elevated spire. Dodge (1955) comments: "A name given to a high spired form which Johnson believed to be identical with the latter's *samarensis* 1915."

martini Dautzenberg 1927. J. Conchyl. 71:53.
Dautzenberg described this form as whitish or flesh colored, ornamented at the top of the last whorl with a transverse orange band. Numerous sets in the Burch collection could be assigned to this form, but all are associated with other forms.

oriola Lamarck 1811. Ann. Mus. Hist. Nat. 16:321.
O. oriola of Lamarck is a black form of *O. oliva* in which the interior is usually lighter and sometimes nearly white. The external black coloration is not always uniform. It is often blended with white spots more or less widespread, which in some specimens occupy half the surface. Sets in the Burch collection from numerous localities could be assigned to this form. Duclos (1835) has represented under the name *O. oriola* several dark examples of *O. reticularia* Lamarck 1811.

samarensis Johnson 1915. Nautilus 29:71.
Johnson stated that his shells were from Samar, Philippines. All were uniform in color representing the dark reticulated form (Thes. Conchyl., fig. 248). The types are in the Academy of Natural Sciences at Philadelphia (no. 111759). We consider this name questionable on all counts.

stellata Duclos 1835. Monogr. *Oliva,* pl. 8, figs. 11, 12.
This form is ornamented with little lines or dots more or less disposed in zigzags. It is devoid

of a transversal zone. Dodge (1955) describes it as "A white form with broad coarse markings, and a shorter spire than in most forms of this species." An interesting series in the Burch collection contains specimens of this color form, and would fit the figure of Reeve (1850, pl. 17, fig. 34*d*), being ivory-white marked sparingly with dashes of violet-brown. However, other color forms are taken from the same locality. Specimens are easily selected from large sets from the Philippines and other localities.

taeniata Link 1807. Besch. Nat. Samml. 2:98. This is a form stated by Link to be distinguished by the dark unicolored band at the upper end of the last whorl. This description is far too inadequate, and in our opinion the name should be ignored.

tigridella Duclos 1835. Monogr. *Oliva,* pl. 8, figs. 13, 14.
This form differs from *stellata* by the pattern of numerous punctations, sometimes isolated, sometimes close together, and aligned longitudinally in zigzags. The background is yellowish gray, rather dark. Dodge (1955) lists this form: "Fawn colored with dark spots." We do not accept the findings of Bridgman (1905), who made a case for the recognition of *O. tigridella* as a distinct species. Reeve (1850), Weinkauff (1878), Tryon (1883), and others have considered it to be a form of the species under discussion. The name has been used by collectors, and specimens of this color form may be selected from large sets from many localities.

Oliva miniacea (Röding 1798). Mus. Boltenianum, p. 33, sp. 391. 6. Das Mergenroth Gmel. V, *Porphyria,* sp. 16 b; Martini 2, t. 45, f. 476, 477, 9 St.

These references are unmistakably to the species long known as *O. erythrostoma* (Meuschen 1787), Mus. Geversianum, p. 376. The work of Meuschen has been officially declared invalid by the International Commission of Zoological Nomenclature in opinions 260 and 261.
It is our opinion that *O. sericea* (Röding 1798) and *O. tremulina* Lamarck 1811 are recognizable distinct species. Johnson (1910)

and others wished to incorporate these species as forms of *O. miniacea.* Typical *O. miniacea* (Röding) is composed of shells ornamented with wavy longitudinal lines, and two transverse bands more or less interrupted, encircling one at the top and one at the center of the last whorl. All, however, are yellow-white, streaked and banded with blue, green, and purple. The aperture is always a deep orange.

O. miniacea is well illustrated in many publications and often as *O. erythrostoma* (Meuschen 1787). Among the more recent publications are those of Kira (1962, pl. 32, figs. 4, 5), and Habe (1966, vol. II, pl. 27, fig. 16).

The species name *porphyretica* Martini 1773, used by some authors, can not be defended because it was not established according to the International Rules. The name was used by Marrat (1871) and was based on a small specimen otherwise close to the typical.

Melvill and Standen (1897) cited an *O. messaris* Duclos 1835 which is perhaps a form of *O. miniacea,* but it is impossible to know exactly the species they intended to designate since Duclos described and figured two very different shells. One (pl. 12, fig. e), which agrees with the description, is a large example of *O. tremulina,* while the other (pl. 22, figs. 7, 8), half as large, is, according to Ducros de St. Germain (1857), a worn and discolored *O. miniacea.*

O. azemula Duclos 1835 should be nullified, as it is based on *O. ponderosa* Duclos 1835, pl. 15, figs. 1, 2, and on an *O. miniacea* without bands (pl. 15, figs. 10, 11).
It is impossible to mention the many color forms of *O. miniacea,* but some of the better known follow.

efasciata Dautzenberg 1927. J. Conchyl. 71: 39.
Dautzenberg named this form on the theory that since Duclos (1835) had first figured an *O. ponderosa* under the name *azemula,* the second figure could not be designated as *O. azemula.* In any event, this is the form without bands which is not uncommon from many localities.

johnsoni Higgins 1919. Nautilus 33:58.
This form is based on Figure 110 of Marrat

(1871). It is a form of dark brown to black color with large white markings. The form is common from many localities, and in colonies merging into other color forms.

marrati Johnson 1910. Nautilus 24:51.
This form is entirely dark brown to black. It is common in many localities.

saturata Dautzenberg 1927. J. Conchyl. 71:39.
This form is described as having darker longitudinal lines, more numerous and the bands more colored, in such a manner that the entire shell has a more sombre aspect. Shells of this description can be selected from almost any long series of specimens from the Philippines and other localities.

sylvia Duclos 1835. Monogr. *Oliva,* pl. 14, figs. 10, 11.
It would seem that the shells generally assigned to this form are orange-yellow with irregular lines, and having two bands of brown usually smaller than in other forms. This color form is quite common in specimens from Zamboanga, Philippines.

Oliva tremulina Lamarck 1811. Ann. Mus. Hist. Nat. 16:310.
The only reference given by Lamarck for *O. tremulina* is the figure of Lister (1685, pl. 727, fig. 14). It is a large shell of which the background is yellowish-white, and is ornamented with heavy longitudinal lines and purplish-brown dots. The last whorl is crossed by two transverse bands of wide blackish dots. The interior of the aperture is fleshy white. *O. nobilis* Reeve 1850, pl. 2, sp. 3 a.b.c., of which the dimensions are exactly those of Lister's figure, and of which the pattern is quite similar, falls into synonymy with typical *O. tremulina.* Johnson (1928:8–9) considered *O. tremulina* to be a form of *O. miniacea* (Röding 1798). A number of authors accepted this conclusion, but it seems to us that the specimens before us labelled *O. tremulina* not only have a fleshy-white aperture, but seem to be less swollen at the posterior or shoulder of the shells. They are otherwise close, but we think that they are easily separable.

Some of the color forms of *O. tremulina* follow.

concinna Marrat 1871. Thes. Conchyl., p. 13, pl. 7, figs. 100, 101.
This form is of a uniform blackish brown, or well sprinkled with a few unusually white spottings more or less triangular. Occasionally, one also sees examples irregularly marked with brown and gray. *O. tenebrosa* Marrat 1871 differs only in the smaller size, which is insufficient to make another form inasmuch as many examples of intermediate sizes are encountered. We think that Johnson (1928) was incorrect in placing *O. concinna* Marrat 1871 with *O. pica* Lamarck 1811 as these shells are very different. Weinkauff (1878) placed *O. concinna* in the synonymy of *O. zeilanica* Lamarck 1811.

A few of the sets before us at this time follow. The shells from Ceylon are larger, lacking the brown edge of the interior lip, marbled with brown and gray. These seem to fit this form. Shells from Bougainville, Solomon Islands, are of uniform blackish brown, some with a few white spottings usually triangular. Large sets from Zamboanga, Philippines, contain shells with all patterns of this form.

chrysoides Dautzenberg 1927. J. Conchyl. 71:139.
This form is a golden-yellow or orange, solid-colored or with a very faint pattern. The slender form and high spire with open suture is very close to the form *zeilanica* (Lamarck) Philippi 1845, from which it differs only in coloration. It is difficult to see why Reeve (1850) and Marrat (1871) united it with *O. irisans* (Lamarck) Duclos 1835, in which the flattened spire is entirely covered by a callosity. Duclos (1844) cited with doubt as forms of *O. tremulina, O. obtusaria* and *O. hepatica,* but it is impossible to identify these names of Lamarck (1811), the descriptions of which are insufficient and which are not accompanied by a reference.

The Burch collection contains sets that fit this form from Zamboanga, Philippines, and also from the Great Barrier Reef, Australia, but the last are larger shells and more slender than those from the Philippines.

Oliva sericea (Röding 1798). Mus. Bolteni-
anum, p. 33, sp. 390.

Röding gave two references. One was to
Martini (1773, pl. L1, figs. 559, 561), which
obviously describes the species known to many
as *O. textilina* Lamarck 1811. The other refer-
ence is to Gmelin (1791, sp. 17, var. 88),
based on Figure 489 of Martini (1773), and is,
according to Pfeiffer (1840), an *O. reticularis*
Lamarck, but it is probably *O. tricolor* Lamarck
because of the black points which adorn the
upper whorls. It is not *O. sericea* in any event.
O. textilina Lamarck 1811 is in the synonymy
of *O. sericea* (Röding 1798). In comparing
O. sericea with *O. tremulina* Lamarck 1811 one
notices that its columellar edge is adorned up
to the top of the aperture by a thick callosity
which spreads wide on the base, and that the
columellar plaits are stronger and less numer-
ous. Its pattern is composed of a multitude
of very fine intercrossed lines which form a
network. The bands also are composed of very
fine and closely knit lines. Finally, the inside
of the aperture, which is white in the back-
ground and barely flesh-colored at the base of
the columella and along the lip in *O. tremulina*,
is entirely light yellow to slightly salmon in *O.
sericea*. The species is well illustrated as *O.
textilina* Lamarck 1811 by Reeve (1850, pl. 6,
fig. 9, a.b.c.). Tryon (1883, pl. 27, figs. 59, 60)
figured the shell well, but in our opinion con-
fused the species with his concept of *O. irisans*
Lamarck 1811. Hirase (1938, 1951, pl. 113,
fig. 1) and Kira (1955, pl. 31, fig. 15) figured
the species well as *O. sericea*.

Specimens matching our concept of this
species may be seen, bearing a monumental
assortment of names, in most of the major col-
lections. It is understandable that many are
confused with *O. tremulina* Lamarck 1811. We
noted a number of sets assigned to *O. sabulosa*
Marrat 1868. We place this name in the
synonymy. The comments of Ford (1953) on
the Liverpool types may be of interest here:
"Two possible syntypes. No locality. 52 mm. ×
22 mm., 40 mm. × 18 mm. I recently found
these shells in a tray with the cut out descrip-
tion of the species. They had not been seen by
Tomlin. G. L. Wilkins has identified them as
young specimens of *O. sericea* (Röding 1798)."

A few of the described color forms of *O.
sericea* follow.

granitella Lamarck 1811. Ann. Mus. Hist.
Nat. 16:314.
Oliva granitella has been regarded by some au-
thors as a distinct species, by others as a
synonym of *O. sericea*, and by Ducros (1857)
and Weinkauff (1878) as a variety of that
species. In comparing the descriptions of
Lamarck, one sees that there are no transverse
bands in *O. granitella*, while *O. sericea* offers
two transverse bands more or less marked,
composed of little brown lines closed in zigzags
and resembling the characters of script. One can
thus suppose that *O. granitella* is a variety of
O. sericea without the bands, but in the absence
of all figuration this interpretation remains
doubtful.

albina Melvill and Standen 1897. J. Con-
chyl. 8:404.
This form, designated as being ivory-white
without other shell characters, may have been
created for an albino specimen of *O. sericea*, as
cases of albinism are known in many species of
olives, but, to be sure of its determination,
we must know in what sense *O. sericea* has
been considered by Melvill and Standen. *O.
sericea, O. tremulina, O. ponderosa*, etc. have
often been considered forms of the same species.
As for *O. sericea* var. *albescens* Johnson 1915,
this can only be an albino form of *O. lignaria*
Marrat 1868. Johnson stated that the spire is
callous.

Oliva lignaria Marrat 1868. Ann. Mag. Nat.
Hist., 4th series, 2:212.

The holotype is in the Liverpool Museum
and was mentioned by Tomlin (1953). A set
of Marrat's types is in the collection of the
Academy of Natural Sciences at Philadelphia,
no. 150597. These are presumably paratypes
and are labelled as coming from Broome,
Western Australia. It seems that the first au-
thor to recognize the distinctive characters of
this species was Ford (1891), in his description
of *O. cryptospira* Ford 1891. It is to be re-
gretted that this name must fall into the
synonymy. The synonymy (as well as color
forms) is extensive, but the two names given

most often by authors are both homonyms: O. ornata Marrat 1867 (not Röding 1798) and O. cylindrica Marrat 1867 (not Borson 1830, nor Sowerby 1850). Reeve (1850), Tryon (1883), and others assigned the species to O. irisans Lamarck 1811. No reference was given to a figure by Lamarck in his description. The fact that the figure of Reeve (1850) does not agree with Lamarck's description in any essential features is quite apparent. Deshayes (1844) refers to Dillwyn (1817). Dillwyn gives one reference to Martini (1773, fig. 561), which is obviously O. sericea (Röding 1798). It is difficult to explain how Reeve (1850) and Marrat (1871) could have united O. tremulina Lamarck 1811 and O. irisans (Lamarck) Duclos 1835, in which the flattened spire is entirely covered with callosity. Tryon (1883) followed Reeve (1850). Kira (1955, 1962) illustrated the species under the name O. ornata Marrat 1867. The typical form from western and northern Australia is slender and white with a fine zigzag pattern in ash to purple-brown. The columella is white, faintly tinged with lilac, the aperture light to deep violet. The color of the interior is not a constant character: a certain percentage of specimens will range from white through light to deep violet. The apex of the Australian form is not as flat and calloused as are those from elsewhere throughout the Indo-Pacific.

A brief comment on a few of the described color forms follows.

albescens Johnson 1915. Nautilus 28:99. This pure-white albinistic form is not rare.

cryptospira Ford 1891. Nautilus 4:135–136. The types are in the Academy of Natural Sciences of Philadelphia. This form is predominantly orange in color. The spire is short with the sutures entirely covered by a heavy callus.

fordi Johnson 1910. Nautilus 24:51. This is the dark brown form. It is common with others from the Philippines, Ceylon, and many other localities throughout the Indo-Pacific.

Oliva vidua (Röding 1798). Mus. Boltenianum, pp. 34, 412, 20, *Porphyria vidua.* Die ungarische Wittwe. Gmel. V, sp. 17, Martini 2, t. 45, f. 472, 473 St.

The figures of Martini are clearly the solid black form of the species known to many as O. maura Lamarck 1811. There has been an interval in which authors have placed this species in the synonymy of O. oliva (Linnaeus 1758). Olsson and Dance (1966) show that the true O. oliva is, in fact, the species known to many as O. ispidula (Linnaeus 1758). The name O. vidua must be restored.

The shape of O. vidua seldom varies. It is relatively a little elongated. The spire is very depressed, often completely flat. A projecting callosity restricts, at the top of the columellar ridge, a scanty canal. This species is remarkable for the richness and variety of the patterns and colors. The typical coloration is a brilliant black, which has attracted the attention of authors.

Reeve (1850, pl. 7, sp. 10a–10g) figured this plate for O. maura Lamarck 1811, and in his listings of synonyms cited three of Lamarck's 1811 species, O. fulminans, O. septuralis, and O. funebralis, and also O. macleaya and O. leucostoma of Duclos (1844). These are all recognized color forms of O. vidua with the exception of O. funebralis and O. leucostoma. However, Reeve did recognize in all figures the details of the spire and shoulder of O. vidua. Tryon (1883) figured the species well as O. maura Lamarck, as did Weinkauff (1878) with the color forms. T. Habe (1966) figured the species well as O. oliva.

Some of the color forms of O. vidua follow.

albofasciata Dautzenberg 1927. J. Conchyl. 71:70. Dautzenberg based this name on a figure of Duclos (1844, pl. 25, fig. 4). The gray background covered with a compact and faint pattern is crossed by two decurrent bands linked by little irregular black swatches.

aurata Röding 1798. Mus. Boltenianum 33. This form is composed of shells with a uniform golden-yellow to orange color. We may add here that, as with other color forms, we have long series showing the gradual merging of one into others.

cincta Dautzenberg 1927. J. Conchyl. 71:63. This form is characterized by dark transverse lines on a background of light yellow, gray, or brown. The author referred to a figure of Reeve (1850, pl. 7, fig. 10e).

cinnamonea Menke 1828. Menke Synopsis 76.

This form is of cinnamon brown color with irregular longitudinal zones of darker brown.

fenestrata Röding 1798. Mus. Boltenianum 34.

This form, based by Röding on Figure 502 of Martini, is distinguished from the form *cincta* by the addition of horizontal lines which cross the vertical lines to create a trellis of quadrangular meshes. Vanatta (1915), instead of using the reference to Martini for the form *fenestrata*, substituted that of Tryon (1883, pl. 23, fig. 23), which represents an individual of the form *cincta*.

macleaya Duclos 1835. Monogr. *Oliva*, pl. 21, figs. 13–16.

This form is gray or yellowish gray covered with lines and inconspicuous compact dots sometimes broken by two unbroken transverse bands.

rumphi Dautzenberg 1927. J. Conchyl. 71: 66.

This form is based on the figure of Rumpf (1705, p. 119, pl. 39, fig. 4). It is ornamented with lines and black spots arranged in the axial plane of the shell.

sepulchuralis Lamarck 1811. Ann. Mus. Hist. Nat. 16:312.

The comments of Dautzenberg (1927), translated from the French, regarding this form may be of interest. "The name *sepulturalis* has been borrowed by Lamarck from the old literature. Rumpf (1705) explains that it means sepulchurae or prinsegraaffnis (funeral of a prince). These olive-like shells are ornamented with spots and black lines arranged in a manner to represent a theory of persons dressed in grand fashion and following the funeral. However, Lamarck has cited as being his *O. sepulturalis* fig. 1, of pl. 365 of the Encyclopedia, on which the pattern is arranged in transverse bands and not longitudinal, as in the figure of Rumpf, while it is the variety b which agrees with the figure. The name *sepulchuralis* should therefore be reserved for the form with the transverse bands, and we propose for the form with longitudinal swatches the name of *rumphi*."

Oliva angustata Marrat 1868. Ann. Mag. Nat. Hist., 4th series, 2:213; Thes. Conchyl., p. 16, pl. 13, figs. 182, 183.

Tomlin (1953) stated: "There are two syntypes in the Liverpool Museum labelled from China. Original of fig. 182, 25 mm. × 12 mm.; shell of fig. 183, 26 mm. × 11 mm. These are very young shells of *Oliva vidua* (Röding)."

Oliva cana Marrat 1871. Thes. Conchyl., p. 15, pl. 11, fig. 152.

Tomlin (1953) stated that the holotype is in the Liverpool Museum from New Guinea, 37 mm. × 15 mm. It is a poor example of *O. vidua*.

Oliva reticulata (Röding 1798). Mus. Boltenianum, p. 33, sp. 396.

Generations of authors have assigned this species to *O. sanguinolenta* Lamarck 1811 (Ann. Mus. Hist. Nat. 16:316: Anim. sans Vert. 7:426). In a discussion of references this name must be used. The references of Röding are: 396.10. *Porphyria reticulata*, Die Netz-dattel. Gmel. V, *Oliva* sp. 17; Martini 2. t. 48, f. 512, 533. 9 St.

Voluta oliva var. *x* was established by Gmelin (1791) first on Plate 739, Figure 28 of Lister (1685–92), which is probably an *O. reticulata* of light coloration; second, on Figure 3 of Plate 39 of Rumpf (1705), which is certainly an *O. sericea* (Röding); and third, on Figures 512 and 513 of Martini (1773), which represent typical *O. reticulata*. Johnson (1928: 11) assumed the role of first reviser and selected the name *O. reticulata* (Röding) for this species on the basis that both Röding and Lamarck used the same figures of Martini. Johnson here abandoned the use of the name *variegata* (Röding). Earlier Johnson (1910:67) had suggested that the name *Porphyria variegata* Röding be accepted for this species. Röding's references for this species are: Mus. Boltenianum, p. 33, sp. 393, 8. *P. variegata*, Die schackigte Dattel. Gmel. *Voluta* sp. 17, 3; Martini 2, t. 45, f. 478, 479. 24 St. This species was based by Röding (1798) on the variety of *Voluta oliva* of Gmelin (1791) which includes, first, an *O. vidua* (Röding) of the form *sepulturalis*,

Knorr (1768, III, pl. 17, fig. 3); second, an *O. vidua* Regenfuss (1758, pl. 1, fig. 2); and third, an *O. vidua* of the form *bifasciata* Martini (1773, fig. 474), and on Figures 478 and 479 of Martini, which are *O. reticulata* of light coloration. Variety a of this *Porphyria* is based by Röding on Figures 480 and 481 of Martini, which represent *O. episcopalis* Lamarck 1811 of the form *lugubris,* and upon the figure of Knorr (1768, v, pl. 19, fig. 1), which is an *O. vidua* of the form *sepulturalis* ornamented with a yellow transverse thread upon the middle of the last whorl. The opinion of the majority of students was that such an assemblage did not justify restoration of the name. The fact remains that it is in use by some authors.

The design of typical *O. reticulata* is composed of lines so close and condensed that it nearly hides the background of the shell. The last whorl is crossed by two blackish bands, and the columella is a beautiful blood-red.

This type has been well figured by Martini (1773, figs. 512, 513), Duclos (1835, pl. 22, fig. 16), Weinkauff (1878, pl. 10, fig. 4), Reeve (1850, pl. 13, fig. 25b), Tryon (1883, pl. 23, fig. 28), and Habe (1966, vol. 2, pl. 27). Habe uses the name *O. variegata* (Röding).

The name *viridescens,* borrowed from Martini by Mörch (1863), H. and A. Adams (1858), Marrat (1871), and others, cannot be used since this is only a part of a descriptive phrase in the work of Martini.

O. pintamella Duclos 1835, which has been regarded by Weinkauff (1878) and Tryon (1883) as a variety of *O. sanguinolenta,* was figured by Duclos in 1835 (Monogr. *Oliva,* pl. 33, figs 7 and 8). It is a small, short shell; the edge of the columella is very callous and strongly folded in throughout the length. The aperture is narrow. Duclos (1844) added for the same species two figures in Chenu (Illus. Conchyl., pl. 35, figs. 9 and 10) which do not agree with the previous ones. Evidently it was these figures that Ducros (1857) considered to be yellow and discolored *O. sanguinolenta.* The true *O. pintamella* (figs. 7 and 8) seems to us to be a good species. Marrat (1771) figured it in Thes. Conchyl., pl. 15, figs. 212 and 213.

A few of the described color forms of *O. reticulata* follow.

azona Dautzenberg 1927. J. Conchyl. 71:109. This form differs from the typical only by the absence of transverse bands.

evania Duclos 1835. Monogr. *Oliva,* pl. 20, figs. 3 and 4. Reeve (1950, pl. 13, figs. 25a and 25b); Marrat (1871, fig. 163); Tryon (1883, vol. 5, p. 79, pl. 23, fig. 29). Ducros (1857) says with reason that *O. evania* is but a form of *O. sanguinolenta* with pale background and strongly banded. It may be added that the pattern is much less closed than that of the form *pallida,* and that the bands are composed of large isolated spots, sometimes nearly black.

pallida Dautzenberg 1927. J. Conchyl. 71:110. This form differs from the typical in that the pattern covers less of the background, giving a lighter aspect to the entire coloration.

zigzag Perry 1811. Perry Conchyl., pl. 41, fig. 4. In this form the pattern consists of longitudinal lines disposed in zigzags and isolated from each other without decurrent bands.

Oliva rubrolabiata H. Fischer 1902. J. Conchyl. 50:409–410, pl. 8, figs. 12 and 13. Type locality, New Hebrides.

A comparison of this species with *O. reticulata* (Röding 1798) would seem logical from form alone, but the folds on the columella are much more numerous, and run the length of the columella to the suture. In addition both the columella and the outer lip are a bright crimson. The body whorl is dark brown, banded with light, close, concentric bands.

This species must be comparatively rare. We have seen only a few specimens. There is a set of two in the collection of the California Academy of Sciences (no. 37876). These specimens match the description and figures in all details. Dautzenberg (1927) reported the species from New Caledonia, but we have seen none from this locality. The Burch collection at this time contains two specimens, both from the New Hebrides, which is the type locality. One is from Tasariki, Espiritu Santo, New Hebrides, from black volcanic sand in about 7 m of water (J. R. Bollard, October 1966), the other from

the north coast of Tanna, New Hebrides, from black volcanic sand (Mrs. H. Dale, August 30, 1966).

Oliva tricolor Lamarck 1811. Ann. Mus. Hist. Nat. 16:316.

The coloring of this species consists of a profuse mottling of clouded blue and saffron-yellow spots with, in most specimens, a large proportion of green, showing two bands, one around the middle of the shell, and one beneath the sutures. But the most characteristic feature of the species is that the spire is obliquely tessellated with black and a slight mixture of red. The aperture is white.

This species has the outline of *O. reticulata* (Röding) and not of *O. elegans* Lamarck. It has the salmon-colored fasciole, but the color of shell is very different from either. The dark specimens are bluish green with bands of slightly darker shade. The entire shell is spotted with yellow; spire and lip are coarsely marked with brown. Light-colored specimens often have bright yellow and blue spots with the bands obsolate. Such specimens often resemble *O. caerulea* (Röding) so closely as to be separated only by the violet-colored aperture of the latter. *O. philantha* Duclos 1835 is a light-colored form approaching *O. caerulea* in external appearance.

This species is common from many Indo-Pacific localities.

Oliva caerulea (Röding 1798). Mus. Boltenianum. *Porphyria caerulea.* Die himmelblaue Dattel. Gmel. V, *Oliva* fp. 17x. Martini 2, t. 48, f. 518. Rumpf t. 39, f. 5. 13 St.

Of the three references cited by Röding the one of Martini (1773, pl. 48, fig. 518) is the only one which agrees with the species. That of Gmelin (1791), *Voluta oliva* var. *x*, is based on three figures: Lister (1685, pl. 739, fig. 28), which is *O. reticulata* (Röding 1798); Rumpf (1705, pl. 39, fig. 3), which is *O. sericea* (Röding 1798); and Martini (1773, figs. 512, 513), which is *O. reticulata* (Röding). The third reference by Röding to Rumpf (1705, pl. 39, fig. 5) represents *O. tricolor* Lamarck

1811 and *O. elegans* Lamarck 1811, but certainly not *O. caerulea.*

This species is known in almost all of the literature as *O. episcopalis* Lamarck 1811. It is unfortunate that we are compelled to accept the *O. caerulea* of Röding, but the name has priority and has been extensively used. It was proposed by H. and A. Adams (1858), and Mörch (1863). Needless to add, the references to the literature, with few exceptions, are to *O. episcopalis* Lamarck.

The typical pattern is a shell covered with scattered punctations mingled with a few little black specks, but in certain examples the spots are grouped in such a manner as to form two interrupted bands situated one at the top, the other about the middle of the last whorl. In others the pattern is transformed into two longitudinal undulations. The aperture is a deep violet.

This is a common species, distributed throughout the Indo-Pacific.

We will mention two of the named color forms.

lugubris Lamarck 1811. Ann. Mus. Hist. Nat. 16:313.
This form differs from the typical by the coloration being darker throughout. The pattern is more marked, and runs into zigzags and large blackish-brown spots. In certain individuals the brown color overruns nearly all the surface, not allowing sight of the white background, which takes the shape of little isolated spaces.

emelliodina Duclos 1844. In: Chenu, Illus. Conchyl., pl. 21, figs. 19, 20.
According to Ducros (1857) this is a peculiar form of the species. The figure of Duclos represents a shell of small size, short, with a spire very little elongated when compared with most specimens.

Oliva atalina Duclos 1835. Monogr. *Oliva*, pl. 10, figs. 9, 10.

Tryon (1883) stated that *O. atalina* Duclos and *O. quersolina* Duclos 1835 are discolored specimens of *O. caerulea* (Röding 1798). Tryon used the name *O. episcopalis* Lamarck. Ducros (1857), while agreeing that *O. quersolina* is a discolored state of *O. caerulea*, was

of the opinion that *O. atalina* is a distinct species. We share his opinion because, despite the resemblance of the pattern of *O. atalina* and *O. caerulea,* the background of the aperture is always white in the first and purple in the second.

Oliva tigrina Lamarck 1811. Ann. Mus. Hist. Nat. 16:322.

This species is based on Figure 475 of Martini (1773), which represents a shell swollen about the top, with a short spire on which the pattern is composed of numerous greenish-gray punctations, and with a few groups of short brown lines. The band is ornamented with black spots, but most specimens are destitute of lines and black spots on the band, and the background is tawny gray instead of white.

Meuschen (1787:370) created a *Cylindrus tigrinum.* This work has been declared invalid but, in any event, Meuschen supported his species by three figures representing olives, of which none is determinable. The name has no meaning.

Marrat (1871) replaced *O. tigrina* Lamarck with *O. holoserica* Martini, a substitution which cannot be accepted since the nomenclature used in the first volume of the Conchylien Cabinet is only occasionally binomial. Furthermore, in the present case, the words *Cylinder holosericus* are used as part of a descriptive phrase. Finally, Martini's species is based on four figures of which only one (Fig. 475) concerns the species in question.

According to Ducros (1857), who examined the type of Duclos, *O. othonia* Duclos 1844 is a young specimen of *O. tigrina* Lamarck.

It is impossible to identify in a satisfactory manner *O. glandiformis* Lamarck 1811. For some authors, this is a variety of *O. tigrina.* The description is quite insufficient, and is accompanied by no reference.

The variety associated by Lamarck, *girol* Adanson 1757, is an entirely different species and already has been named *O. flammulata* by Lamarck himself.

We mention one of the named color forms frequently used by authors.

fallax Johnson 1910. Nautilus 24:64.
In this form the bands are suffused and cover the entire shell. We noted Johnson's type in the Academy of Natural Sciences of Philadelphia. It is the common all-black color form. It may be mentioned that this form is often confused with the black form of *O. vidua* (Röding), but the shell is much less cylindrical in outline, and the sutural callus is less elevated.

Oliva elegans Lamarck 1811. Ann. Mus. Hist. Nat. 16:312.

The shell is olive or brownish yellow closely covered with zigzag lines or punctations or both, varying from chocolate to nearly black. The fasciole is salmon-colored. This species seems to be confusing to many, with other species being assigned to it in error. It is separable from *O. tigrina* Lamarck 1811 and *O. tricolor* Lamarck 1811 by the shorter and more tumid growth, and the erect callous production of the last whorl upon the spire, which is proportionally depressed. Although this species is smaller, it has the more cylindrical form and elevated sutural callus of *O. vidua* (Röding 1798). Light-colored specimens with the bright salmon-colored fasciole resemble in a general way *O. reticulata* (Röding 1798). It also has a range in color similar to that of the latter species, and lacks the dark fulvous and melanic forms of *O. vidua* (Röding). Small dark specimens are often very close to specimens referable to *O. funebralis* Lamarck 1811. This species is common, with a wide distribution throughout the Indo-Pacific.

Oliva lecoquiana Ducros 1857. Revue Critique, p. 43, pl. 2, figs. a–c.

The shell is banded with chocolate-colored triangular markings, as in *O. elegans* Lamarck 1811. The fasciole is stained with saffron. The form is somewhat more bulbous, and the interior of the aperture is violaceous.

O. similis Marrat 1867 is a minor form of *O. lecoquiana. O. calosoma* Marrat 1871 (not Duclos 1835) is a small form.

We have specimens that fit the description of *O. lecoquiana* from Madagascar, Fiji Islands, and other localities.

Oliva calosoma Duclos 1835. Monogr. *Oliva,*
    pl. 26, figs. 1, 2.

Tryon (1883) describes the species as "Pure
white, or with slight indications of three bands
composed of occasional triangular brown mark-
ings. Length 27 mm. China." Weinkauff
(1878) accepted the species.

Oliva bulbiformis Duclos 1835. Monogr. *Oliva,*
    pl. 27, fig. 10.

The shell is short and very bulbous, colored
as *O. elegans* Lamarck 1811, but the interior of
the aperture is chocolate brown. Reeve (1850)
figured and described *O. bulbiformis,* but
mentioned *O. dactyliola* Duclos 1835 and
O. caroliniana Duclos in the synonymy. We do
not accept this (see below).

This is a common species from many
localities throughout the Indo-Pacific.

Oliva dactyliola Duclos 1835. Monogr. *Oliva,*
    pl. 27, figs. 5–8.

We have eliminated from the synonymy
Figure 9 of Duclos. It presents no well-defined
character, and Ducros (1857), who studied the
shell represented by this figure, stated that it is
O. bulbiformis Duclos and not *O. dactyliola.*
Reeve (1850) supposed that *O. dactyliola* could
be a synonym of *O. bulbiformis* Duclos, and
Tryon (1883) made it a variety of *O. funebralis*
Lamarck, to which he compared, moreover,
O. picta Reeve and, with doubt, *O. blanda*
Marrat. Finally, Johnson (1910), although
maintaining that *O. dactyliola* is a distinct
species, said that it appears to be intermediate
between *O. funebralis* Lamarck and *O. bulbi-
formis* Duclos, having the spire of the first and
the form of the second. Sowerby (1900)
accepted the species with the statement that he
had specimens from Pondoland and also from
Cebu, Philippines. We have specimens from the
Philippines, New Guinea, Indonesia, New
Caledonia, and elsewhere that agree well with
the Figures 5–8 of *O. dactyliola* Duclos.

Oliva funebralis Lamarck 1811. Ann. Mus.
    Hist. Nat. 16:332.

The shell is more cylindrical than *O. bulbi-
formis* Duclos. It differs from *O. lecoquiana*

Ducros in that the lower band of the fasciole is
deeply strigated with chocolate. The aperture is
slightly bluish or chocolate. Johnson (1910)
stated that this species seems to occupy an
intermediate position between *O. tigrina*
Lamarck and *O. elegans* Lamarck. It is
beautifully illustrated by Marrat (1871, pl. 11,
figs. 143–148) under the name *leucostoma*
Duclos 1835 and *labradorensis* (Röding 1798).
The figure attributed by Röding to Lister (1685,
tab. 731, fig. 20) is unrecognizable, and so
labradorensis can be dropped. The narrower
form suggests a relationship to *O. mustellina*
Lamarck, while the broader form shows a ten-
dency toward the more inflated *O. dactyliola*
Duclos. Johnson (1915) discussed the species
again, stating that it is extremely variable, with
limits which are difficult to define. Reeve (1850,
pl. 7, sp. 10) figured a specimen of this species
which he considered a form of *O. vidua*
(Röding). Tomlin (1953) considered *O. leu-
costoma* Duclos to be separable from *O. fune-
bralis,* but we are disposed to place it in the
synonymy. Some authors have thought the
following species of Marrat (1871) to be
valid, but we think that they belong in the
synonymy of *O. funebralis*: *O. clara, O. pro-
pinqua, O. lutea,* and *O. inornata.*

It is probable that further study will indicate
that this is one entity including a number of
related forms.

Oliva similis Marrat 1867. Ann. Mag. Nat.
    Hist., 3rd series, 20:215. Thes. Conchyl.
    pl. 14, figs. 205, 207.

Tomlin's comments on the shells in the
Liverpool Museum follow: "Four (not types).
Eastern seas. Max. 35 mm × 16 mm, Min.
31 mm × 14 mm. Av. 32.2 mm × 15 mm.
I do not think the shells numbered 206 and 207
are the originals of these figures. None of the
four seem to fit any of the three figures that
Marrat gives of *O. similis* though they are that
species right enough." Weinkauff (1878, pp. 27,
7, 7, 11, sp. 10) accepted the species. At first we
thought to place this species in the synonymy of
O. bulbiformis Duclos 1835 but, after seeing
more specimen material, we are now disposed
to admit the species. A few sets noted are: Acad.
Nat. Sci. Philadelphia, no. 128327 and 15853

from Ceylon, and 104786 from New Guinea; Am. Mus. Natl. Hist. no. 48428 from Singapore. The specimens are white or cream in color, the pattern is somewhat as in *O. scripta* Lamarck, the size about 32 mm. All seem to be more cylindrical than *O. bulbiformis*. All have a violaceous aperture.

Oliva laevis Marrat 1871. Thes. Conchyl. p. 4, pl. 20, figs. 330–331.

Tomlin (1953) states that the holotype only is in the Liverpool Museum. It is from the Seychelles, 18 mm × 7 mm. A very young shell of *O. similis* Marrat (spelled *laevis* on page 26, *laeve* on caption to plate). Weinkauff (1878) thought it to be a juvenile *O. elegans* or *O. tigrina*. The confusion here is apparent.

Oliva caroliniana Duclos 1835. Monogr. *Oliva*, pl. 19, figs. 5, 8.

This species is close to *O. mustellina* Lamarck 1811. The shells are more bulbous and the spire more exserted. Weinkauff (1878) and Marrat (1871) accepted the species. Sets so labelled in the major collections are of interest. Acad. Nat. Sci. Philadelphia, no. 15855 from Singapore, and set no. 104782 from Mauritius are the same.

Oliva mustellina Lamarck 1811. Ann. Mus. Hist. Nat. 16:316.

The shell is cylindrical, the aperture long and narrow, the spire short. The color is a pale yellow covered with light chestnut figurations. The interior of the aperture is a deep violet. Many specimens in the large museum collections seem to be assigned to this species in error. It is surprising to note so many assigned to the quite different *O. elegans* Lamarck. Variation in one biological entity or grouping of several related species are possibilities to consider in this as well as other species in this family. Specimens from Japan, China, Singapore, India, and the Philippines seem to be typical. We place the following species tentatively in the synonymy.

Oliva pacifica Marrat 1871. Thes. Conchyl., p.15, pl. 11, fig. 151. Some authors have accepted *O. pacifica* as valid. Weinkauff (1878) accepted the species and placed *O. arctata*

Marrat in the synonymy. Shell labelled from China.

Oliva arctata Marrat 1871. Thes. Conchyl., sp. 99, p. 20, figs. 229, 230. The holotype only is in the Liverpool Museum, labelled China Sea, 25 mm × 10 mm. Tomlin (1953) stated that this is obviously the young of *O. pacifica* Marrat.

Oliva ponderosa Duclos 1835. Monogr. *Oliva*, pl. 15, figs. 8, 9.

The shell is cream-white, slightly colored with obscure bluish or violet short interrupted streaks, and a few brown reticulations. The columella and interior of the aperture is carnelian-white, sometimes tinged with flesh-pink. The shell is thick and stout, with the spire but little exserted. The last whorl is more or less produced toward the apex. Long sets from Mauritius, Seychelles, Maldive Islands, and other localities of the Indian Ocean produce shells with both white and light-salmon apertures. The high callosity above the suture becomes less pronounced in the more juvenile specimens. The pronounced growth of the last whorl in all adults of this form, and the consistently more obese shape leads us to admit the species. Other species are considered distinct on grounds much less apparent.

The species was well illustrated by Reeve (1850), Weinkauff (1878), and Marrat (1871).

Oliva rufula Duclos 1835. Monogr. *Oliva*, pl. 19, figs. 9, 10.

The shell is fawn colored, crossed diagonally or transversely by dark-chestnut bands formed by the coalescence of trigonal markings. The aperture is white.

This species seems to maintain both form and pattern consistently, showing no noticeable variations. It is distinctive and easily recognized. This is a fairly scarce shell. Most specimens come from the Philippines.

Oliva scripta Lamarck 1811. Ann. Mus. Hist. Nat. 16:315.

The shell is yellowish brown with pale chestnut zigzag markings, and two bands of

brown waved characters. The shell is cylindrically ovate with a short spire.

All authors agree about the similarities of this species with some forms from the West Indies. At times it is difficult to separate *O. scripta* from specimens of the West Indies called *O. jamaicensis* by Marrat (1871) and *O. caribbensis* Dall and Simpson 1901. The subcylindrical form a little bulging at the top of the last whorl, the short spire, the pattern and color are identical. The pattern of *O. sayana* Ravenel 1834 from the western Atlantic resembles that of *O. scripta,* but the form is more elongate, the spire higher, and the last whorl is not swollen above. It is our opinion that *O. scripta* may be easily separable from the above forms by the fact that the produced posterior of the last whorl gives the shell more the shape of *O. mustellina.* The species was well illustrated by Reeve (1850) and by Tryon (1883). Kuroda and Habe (1952) listed the species from Japan.

We have this species from China, Ceylon, the Moluccas, and from Thailand. We also have sets from the Cook Islands that seem to be identical.

Oliva annulata (Gmelin 1791). Syst. Nat., ed. 13, p. 3441.

This species is listed widely in the literature as *O. emicator* (Meuschen 1787). Meuschen's names have been declared invalid by the International Commission. The name *O. guttata* Lamarck 1811 has also been used by many authors.

It is unfortunate that the first available name for this species seems to be *O. annulata.* This name was given to an abnormal ringed shell. The color is entirely white and the shell is characterized by a protruding ring encircling the middle of the last whorl. The ring is not uncommon in this species. We have many specimens of all color forms with this character. We know the shell from the figure of Lister (1685), and that of Martini (1773), the last having been copied by Wood (1828) in the Index Testalogicus.

Vanatta (1915) cited as representing typical *O. annulata* Figure b of Plate 16 of Duclos, and Figure 60 of Plate 5 of Marrat. Both figures represent a yellow-orange shell, without a ring in the middle of the last whorl. This is completely wrong, since it is especially the ring which characterizes the *O. annulata* of Gmelin.

O. leucophaea Lamarck 1811 is an absolute synonym. It is odd that Lamarck substituted the name for *annulata,* even though he cited it among the references to his species.

Some of the named color forms follow.

amethystina (Röding 1798). Mus. Boltenianum, p. 35.

This should perhaps be recognized, as this represents the common color which is ornamented with round, purple spots, fairly regularly spaced on a clear flesh-colored background.

alba Sowerby 1825. Cat. Tankerville, p. 86.

The shell is entirely white inside and out.

carnicolor Dautzenberg 1927. J. Conchyl. 71:22.

The background is yellowish white without spots. The dorsal region of the last whorl is reddish pink.

intricata Dautzenberg 1927. J. Conchyl. 71:23.

This form differs in the pattern of a compact confusion of little brownish lines sprinkled throughout with black dots. The white background appears between the meshes of the network in the shape of little gaps more or less triangular.

mantichora Duclos 1835. Monogr. *Oliva,* pl. 15, figs. 7, 8.

The form *mantichora* presents at the top of the last whorl an angle more or less pronounced. The pattern and coloration resemble those of the form *intricata,* but there are also examples of which the background is more open. Marrat (1871, pl. 5, fig. 29) shows an individual in which the keel, situated lower down, tends to approach that of the typical *annulata,* but this keel is blunt and does not have the aspect of a ring.

nebulosa Dautzenberg 1927. J. Conchyl. 71:22.

This form was figured by Reeve (1850, pl. 14, species 30g) as *O. leucophaea* Lamarck. The

spots have the character of scattered triangular blotches, and the ground is of a ruddy tinge.

O. *annulata* (Gmelin) is a common species distributed throughout the Indo-Pacific. We have sets of mixed and intergrading forms from Tahiti, Solomon Islands, Guam, New Guinea, Marquesas, Mauritius, Admiralty Islands, and many localities in the Philippines.

Oliva carneola (Gmelin 1791). Syst. Nat., ed. 13, p. 3443.

The figure of Martini (1773, fig. 495) upon which Gmelin based this species is very poor, but one can still recognize that it concerns a shell with reddish background crossed on the last whorl by bluish-gray bands running downward. This coloration may be regarded as typical.

O. *carneola* is either short or elongate, either swollen or cylindrical; the spire is constantly covered with a thick callosity which completely hides the superior whorls, that of the last whorl alone being free. The pattern and coloration give this species a great number of modifications, and change so often during growth that it is impossible to place the shells into determined color forms. We will mention a few of the most characteristic.

We have avoided discussion of generic names in *Oliva*. The differences in radula or anatomy are slight, and we see no systematic advantage in the recognition of such names in this group. For example, some authors place this species in the genus *Galeola* Gray 1858.

This is a common species throughout the Indo-Pacific. Inasmuch as many or all of the described color forms appear in most of a large series from all localities, it seems futile to attempt a division of them. A few of the named color forms follow.

adspersa Dautzenberg 1927. J. Conchyl. 71:9. The shell is irregularly sprinkled with numerous small, white, rather conspicuous triangular flecks.

bizonalis Dautzenberg 1927. J. Conchyl. 71:8. This shell has a red background crossed in the middle of the last whorl by two white bands rather large and close. (See Duclos 1844, pl. 28, fig. 13.)

candidula Dautzenberg 1927. J. Conchyl. 71:8.
The bands are barely visible at the beginning of the last whorl and disappear completely thereafter. (See Duclos 1844, pl. 28, figs. 12, 16.)

coccinata Dautzenberg 1927. J. Conchyl. 71:8.
The shell is a nearly uniform red, with bands visible. (See Duclos 1844, pl. 28, fig. 8.)

trichroma Dautzenberg 1927. J. Conchyl. 71:9.
The shell differs from *unizonalis* by the presence at the summit of the last whorl of a deep-purple band at the suture which imparts to the shell a three-colored aspect.

unizonalis Dautzenberg 1927. J. Conchyl. 71:9.
The shell has a red background crossed by one large white band in the middle of the last whorl. (See Duclos 1844, pl. 28, figs. 6, 14.)

Oliva athenia Duclos 1835. Monogr. *Oliva,* pl. 26, figs. 17, 18 (excl. 19, 20).

O. *athenia* is a well defined species, characterized by the squat form, the spire nearly flat and mucronated in the center. Nevertheless, it has often been misunderstood. Duclos himself, after correctly representing it on Plate 28, Figures 17, 18, has added under the same name Figures 19 and 20, which are of O. *mucronata* Marrat and O. *faba* Marrat. Tryon (1883) considered it a synonym of O. *sidelia* Duclos 1835.

A typical O. *athenia* is ornamented with longitudinal blotches standing out clearly in zigzags on a tawny background. These blotches are either separated or approximate. In certain examples they stand out on a dotted or obscurely reticulated background. We have specimens from New Caledonia, Andaman Islands, Fiji Islands, and Australia.

This species has been the source of much disagreement. Reeve (1850) placed it in the synonymy of O. *carneola* (Gmelin 1791).

Johnson (1910) said under his discussion of O. *mustellina* Duclos, "O. *athenia* Duclos resembles this species in miniature." Johnson's comment might be in order if one failed to

note the spire. We think that it is distinct. Most of our specimens were received labelled *O. faba* Marrat 1867, a name which we now place in the synonymy.

Oliva sidelia Duclos 1835. Monogr. *Oliva*, pl. 19, figs. 1, 2. Duclos (1844, p. 23, pl. 21, figs. 1, 2). Ducros (1857, p. 69). Marrat (1871, pl. 15, figs. 231, 232) (a copy of the figures of Duclos). Tryon (1883, pl. 33, figs. 27, 44) (a copy of the figures of Duclos).

Tryon (1883) united, under the name *O. sidelia, O. volvaroides* Duclos 1835, *O. lepida* Duclos 1835, and *O. todosina* Duclos 1835. We share his opinion for *sidelia, volvaroides, lepida,* and *todosina,* but it is our opinion that *athenia, mucronata,* and *faba* constitute a distinct species, more squat, with a more depressed spire, and closely mucronated in the middle. The pattern is much plainer and darker. Finally, *sidelia, volvaroides, lepida,* and *todosina* have the last whorl separated by a suture greatly canaliculated, while in *athenia, mucronata,* and *faba* the suture of the last whorl is deep but very tight. We find ourselves presented with two distinct species, *sidelia* and *athenia.* It is to be regretted that the name *sidelia,* which was created for a young shell, should have been selected for this species. *O. volvaroides, O. lepida,* and *O. todosina* apply to adult specimens. The type of *O. sidelia* is a shell 10 mm in length, white, with faint violet undulations, and having on the dorsal region a large brown spot which occupies nearly the whole length of the last whorl, except for a white zone close below the suture. This coloration must be infrequent, since Marrat (1871) and Tryon (1883) copied the figures of Duclos. Weinkauff (1878) gave three figures of *O. sidelia,* but this interpretation is difficult, the author admitting that they are not elongated enough, and that the relation between the height and width is not exact. Reeve (1850, pl. 22, sp. 59) figured and described *O. volvaroides.*

Specimens from China, Mauritius, Seychelles, Solomon Islands, and other localities indicate a distribution throughout the Indo-Pacific. A few forms of this species follow.

lepida Duclos 1835. Monogr. *Oliva*, pl. 25, figs. 15 to 20.

The shell has a pattern of triangular spots. We have specimens that may fit this form from Mauritius, Seychelles, China, and the Philippines.

todosina Duclos 1835. Monogr. *Oliva*, pl. 25, figs. 9, 10.

This form was based by Duclos on a shell of which the pattern and especially the middle band of the last whorl are darker. The habitat of California indicated by Duclos is certainly erroneous.

volvaroides Duclos 1835. Monogr. *Oliva*, pl. 25, figs. 11 to 14.

The type of *O. volvaroides* represented by Duclos (pl. 25, figs. 11 and 12) is coffee-and-cream colored with some transverse lines hardly visible. His Figure 13 is of a variety entirely white, and Figure 14 is of a uniform blackish brown which is so similar to Figure 20 (inscribed as a variety of *lepida*) that one might be tempted to believe that these two figures were made from the same shell. While maintaining *O. volvaroides* as a species, Ducros (1844) said that a study of a great number of individuals from diverse localities might authorize a reunion with *O. lepida.*

Oliva tessellata Lamarck 1811. Ann. Mus. Hist. Nat. 16: 320, b. 28.

The shell is yellow, spotted with purple. The aperture and columella are deep violet.

Dillwyn (1817) and Marrat (1871) took the name *O. tigrina* (Meuschen 1787) for this species. Meuschen's names have been declared invalid by the International Commission, but in any event it is an obvious error because no reference cited in the Museum Geversianum relates to *O. tessellata.*

O. tessellata varies only in the number of punctations with which the surface is ornamented. In adult specimens they deviate rarely on the end of the last whorl. The dark purple of the interior is constant.

Some authors place this in the genus *Neocylindrus* Fischer 1883, with *O. tessellata* Lamarck as the type.

This is a common species distributed throughout the Indo-Pacific.

Oliva bulbosa (Röding 1798). Mus. Bolteni-anum, p. 34, *Porphyria bulbosa.*

It is to be regretted that the vagaries of the system permit no escape from abandoning the name *O. inflata* Lamarck 1811 under which this well known species has been recognized for generations. It is needless to add that almost all of the following references to the literature are the work of authors who knew the species as *O. inflata* Lamarck.

Both Röding (1798) and Lamarck (1811) refer to the same figures of Martini (Conchyl. Cab. II, tab. 47, figs. 507, 508). These figures represent specimens having undulating longitudinal stripes of brown. Hence we must accept this form as typical.

The form of this species is very characteristic: swollen gibbous growth, fasciole with a heavy callous ridge which is independent of the columellar plaits. This is the only species of *Oliva* with this character.

Inasmuch as most of the large sets in collections from various localities seem to contain specimens of almost all of the described forms, it seems futile to consider them in great detail. However, a few will be mentioned to give the references.

bicingulata Lamarck 1811. Ann. Mus. Hist. Nat. 16:94. *bicincta* Lamarck 1822.
Two revolving dark lines are present.

fabagina Lamarck 1811. Ann. Mus. Hist. Nat. 16:94.
The bands fuse and cover irregularly the greater portion of the shell. This form was figured by Marrat (1871) as *O. crassa* Martini.

immaculata Vanatta 1915. Nautilus 29:68.
This is the white albino form. In some collections this form is labelled *O. alba* Dillwyn 1817.

inflata Lamarck 1811. Ann. Mus. Hist. Nat. 16:310.
Specimens with only the small uniform bluish-gray spots.

lacertina Quoy and Gaimard 1825. Voy. Uranie, p. 432, pl. 72, figs. 4, 5.
This is a peculiarly banded color form of this species.

This species is generally distributed throughout the Indo-Pacific. We have large sets from Mozambique, Zanzibar, the Red Sea, Mauritius, Suez, Tanzania, Singapore, Indonesia, etc.

Oliva paxillus Reeve 1840. Conchol. Icon., pl. 21, sp. 56, a, b.

The shell is cone shaped, yellowish white in color, smooth, with triangular brown markings forming interrupted bands, and spots beneath the sutures and on the fasciole. The interior of the aperture is sometimes two- or three-banded, but this is not a constant character.

We are accepting the opinion of the late J. R. le B. Tomlin (1934), a very careful observer, who studied the types of all of the species involved. We also studied the types. All of them are in the British Museum (Natural History).

Omogymna was described by von Martens (1897) as a subgenus of *Oliva,* with *O. paxillus* Reeve as the type. Tryon (1883) pointed out that *O. nitidula* Duclos 1835 is preoccupied by *nitidula* Dillwyn 1817 (not Gmelin 1791). *Oliva ozodona* Duclos 1835 is certainly not *O. paxillus.* On the other hand, *Oliva sandwichiensis* Pease 1860 and *Oliva thomasi* Crosse 1861 are both the same as *O. paxillus* Reeve.

While not common, the species seems to be rather generally distributed. It seems to be the only species of *Oliva* from the Hawaiian Islands.

We have specimens from various localities in the Indian Ocean, and from Okinawa, Guam, Marshall Islands, etc.

Oliva duclosi Reeve 1850. Conchol. Icon., pl. 19, sp. 44.

The shell is orange-yellow, thickly reticulated with olive-brown, the spaces of the network being rather distant and sharply triangular. The columella and interior of the aperture are orange-yellow.

It is difficult to know how so many authors have confused this species with *O. paxillus* Reeve 1850. *O. duclosi* has been reported from numerous Pacific localities, but it is more common from Tahiti and neighboring islands.

According to Ducros (1857), *O. natalia*

Duclos 1844 is typical *O. duclosi,* but blighted and discolored, and his figure is enlarged, too red, and embellished to suit. Ducros studied the type. The same author considers *O. stainforthi* Reeve 1850 to be a squat specimen of the form *lentiginosa* Reeve 1850.

We wish to mention the two following names as color forms of *O. duclosi* because both are occasionally seen in the literature. Both are placed in the synonymy.

lentiginosa Reeve 1850. Conchol. Icon., pl. 19, sp. 45, a.b.

This seems to be no more than a lighter-colored specimen.

esiodina Duclos 1844. In Chenu, Illus. Conchyl., p. 18, pl. 16, figs. 19, 20.

This form or species is questionable, but it is obvious that if it is possible to identify *O. esiodina,* and that it is conspecific with *O. duclosi,* the name of Duclos has priority. We have failed to locate even one locality record.

The shell is very thick with the spire exceptionally elevated. We know this only from the figures of Duclos, of which one has been reproduced by Tryon (1883).

Oliva panniculata Duclos 1835. Monogr. *Oliva,* pl. 15, figs. 15, 16. In Chenu, Illus. Conchyl., p. 12, pl. 6, figs. 15, 16.

The pattern of *O. panniculata* represented by the Figures 15 and 16 of Duclos is composed of very fine longitudinal lines of a light fawn color. The last whorl is crossed, a little below the middle, by a narrow band of gray spots, and by another of the same color under the suture. Figure 17 of Duclos represents a form slightly more slender, and Figures 19 and 20 an example in which the last whorl is crossed by two decurrent gray bands.

Some references to this species are: Reeve (1850, pl. 26, sp. 77); Tryon (1883, pl. 32, figs. 24, 25); Ducros de St. Germain (1857, p. 64); Marrat (1871, p. 10, figs. 83, 84); Weinkauff (1878, p. 84, pl. 22, figs. 10, 11, 12).

Marrat (1871) figured under the name *O. panniculata* an exceptionally large shell ornamented with a highly-colored pattern. Schepman (1911) listed the species with comments on variation. Melvill and Sykes (1896) reported the species from the Andaman Islands.

Melvill and Standen (1897) described a variety *williamsi* as one having the pattern more sharply marked and farther apart as well as by the absence of a band on the last whorl.

While not a common species, this has a wide distribution. We have it from Andaman Islands, Thailand, Madagascar, Mauritius, and Ceylon.

We place the following species in the synonymy of *O. panniculata: O. ozodona* Duclos 1835, Monogr. *Oliva,* pl. 5, figs. 19, 20. In studying the work of Duclos, we note that he figured the species under discussion on Plate 5, Figures 15 to 18 (which are *O. panniculata*), and that Figures 19 and 20 on the same plate are *O. ozodona.* They are very similar in all characters observable in Duclos' fine color plate.

Oliva concavospira G. B. Sowerby 1914. New mollusca of the genera *Pleurotoma* (*Surcula*), *Oliva,* and *Limopsis* from Japan. Ann. Mag. Nat. Hist., 1914, ser. 8, 13: 445, pl. 18, fig. 2.

The sunken spire of this species seems to be a constant character. The spire is sunk in a concavity below the shoulder of the last whorl.

Excellent color figures of the species showing both views were given by Kira (1955, p. 63, pl. 31, fig. 6), and Kira (1962, pl. 32, fig. 6).

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Revision of the Genus *Pandanus* Stickman, Part 23
Three Australian Species of *Pandanus*

Harold St. John[1]

THE SECTION *Microstigma* of the genus *Pandanus* has but three representatives in Australia. *P. de-Lestangii* Martelli was the first of these to be discovered and described.

P. adscendens St. John belongs in the large section *Pandanus*. Like many others of its species, this new one with smooth-sided phalanges has its habitat on the marine littoral.

P. darwinensis St. John was described earlier and the details of its phalanges were given. Now habit photos are at hand and they show vegetative and fruiting structures.

Pandanus de-Lestangii Martelli, Roy. Soc. Queensl. Proc. 38(5):57–58, pl. XI, 1926 (sect. *Microstigma*).

  P. aquaticus F. Muell., Kew J. Bot. 8:324, 1856 (nomen provisorium); Fragm. Phytog. Austral. 5:40, 1865; and 8:220, 1874; Bentham, Fl. Austral. 7:149, 1878; Warburg, Engler's Pflanzenreich IV, 9:85, 1900; S. T. Blake, Austral. J. Bot. 2(1):130–132, pl. 7, fig. 3, 1954.

Figs. 240 and 241

DIAGNOSIS OF HOLOTYPE: Small and tree-like, forming dense clumps; trunk to 5 m in height, near the top 2–3-branched; prop roots numerous; each soon producing a new stem; leaves 1.8–2.7 m long, 7.5–8 cm wide near the base, 5.3 cm wide at the middle, bluish green, drooping, coriaceous, broadly channeled above the midrib, with 2 lateral pleats, at midsection with 62 parallel secondary veins in each side, throughout the lower side the tertiary cross veins conspicuous, forming long oblong meshes, the blade sword-shaped and from the base gradually tapering to the trigonous subulate unarmed apex which is about 15 cm long, this at 10 cm down 3.5 mm wide; the base amplexicaul and unarmed, but beginning about 6 cm up

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the margins with prickles 2.5–3.5 mm long, 5–12 mm apart, slender arcuate subulate, appressed ascending, reddish tipped; the midrib below in lower and outer thirds unarmed; at midsection the margins with prickles 1.5–3.5 mm long, 10–17 mm apart, arcuate subulate, appressed ascending; the midrib below narrow, sharp, with prickles 2–3 mm long, 18–35 mm apart, slender subulate, closely appressed ascending; the apex almost unarmed; pistillate plant blooming in late October or early November, with 1–2 terminal syncarps; when ripe the syncarps 10–13 cm in diameter, broadly ellipsoid, 3-sided, green, at maturity the core in a few days shrinks to a remnant 7 cm long, 2.5 cm in diameter, and the drupes fall in a mass; drupes very numerous, 31–35 mm long, the abundant 1-celled ones 7–11 mm wide, 6–8 mm thick, narrowly oblanceoloid, upper ¼ free, 5–6-angled, the sides smooth, somewhat shiny, gently curving, the apex rounded pyramidal; stigma 1.5–2 mm long, broadly ellipsoid, creased, flush, oblique, excentric, brown, papillose; drupes with 1 cell are the normal, for on the holotype (FI) there are 136 such, and 21 with 2 cells, and 1 short basal one with 3 cells, while in the isotypic specimen (BRI) there are 173 with 1 cell, to 32 with 2 cells, and 1 short basal one with 3 cells. Martelli recorded ones with 4 or 5 cells. Of the 2-celled ones, 6 appeared to have a third stigma, but this was actually a corky scar, and the fruits had only 2 cells. The 2-celled drupes are 10–14 mm wide, the apex shallowly lobed, the cleft 1–3 mm deep, the stigmas 0.8–1 mm long, ellipsoid to obovate, horizontal or oblique, centripetal; the single 3-celled drupe (a short basal, asymmetric one) 26 mm long, 14 mm wide, 12 mm thick, deltoid-oblanceoloid, the stigmas centripetal, placed in a triangle; the 1-celled drupes with the endocarp central, bony, pale, the lateral walls 0.8–1.3 mm thick, the apex subtruncate; seed subcuneate-barrel-shaped, 7–8 mm long; the
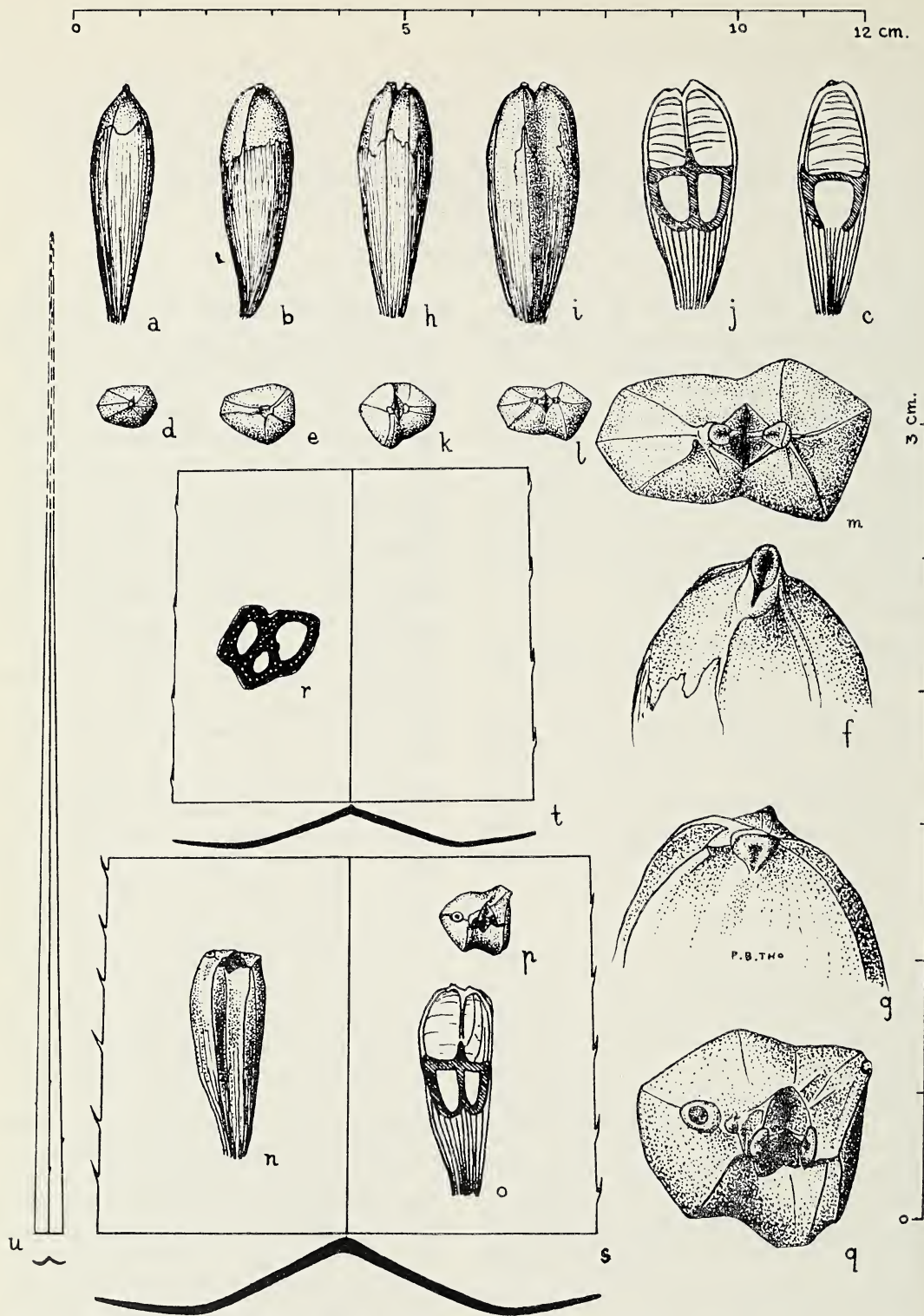
FIG. 240. *Pandanus de-Lestangii* Martelli, from isotype. *a, b,* 1-celled drupes, lateral view, × 1; *c,* drupe, longitudinal median section, × 1; *d, e,* drupes, apical view, × 1; *f, g,* drupe apex, oblique view, × 4; *h, i,* 2-celled drupes, lateral view, × 1; *j,* drupe, longitudinal median section, × 1; *k, l,* drupes, apical view, × 1; *m,* drupe, apical view, × 4; *n,* 2-celled drupe, lateral view, × 1; *o,* drupe, longitudinal median section, × 1; p, drupe, apical view, × 1; *q,* 2-celled drupe, with corky scar imitating a third stigma, apical view, × 4; *r,* 3-celled drupe, transverse section, × 1; *s,* leaf base, lower side, × 1; *t,* leaf middle, lower side, × 1; *u,* leaf apex, lower side, × 1.
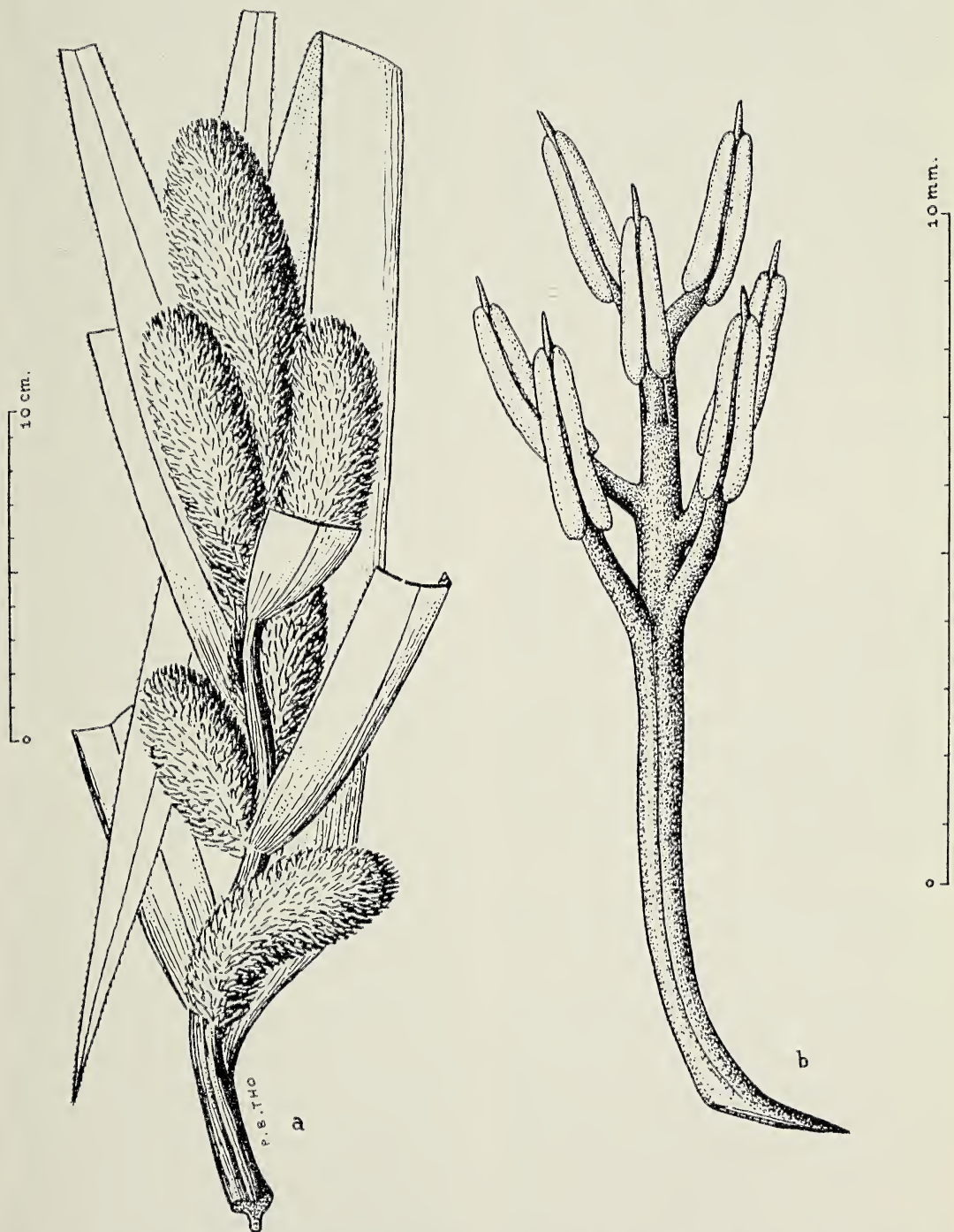
Fig. 241. *Pandanus de-Lestangii* Martelli, from type locality, 6 Nov. 1926, *de Lestang. a,* Staminate inflorescence, × ½, *b,* fascicle of stamens, × 10.

2-celled drupes with the seeds median, similar but slightly oblique and 4 mm in diameter; apical mesocarp with numerous transverse, pale membranes; basal mesocarp fibrous and fleshy.

DESCRIPTION OF STAMINATE PLANTS: Growing mingled with the pistillate plants; plants blooming in October and November, bearing 1–2 staminate inflorescences, these with numerous pale leafy bracts, the median ones 31 cm long, 3 cm wide, ligulate, acute, firm, foliaceous, veiny, the middle and upper margins with ascending prickles 0.2–0.3 mm long, about 1 mm apart; spikes 3–6 cm long, 12–15 mm in diameter, finger-like, dense; fascicles of stamens about 15 mm long, divergent, the common filament base 7–10 mm long, bearing 4–7 stamens; free filament tips 0.5–2 mm long; anthers 2–2.9 mm long, oblong, bearing a subulate projection of the connective 0.5–0.6 mm long.

HOLOTYPE: "Australia; growing under palms along perennial streams about 200 miles southwest of Burketown (Burke District), Northwest Western Queensland," Albert de Lestang (FI)! Isotypes (BRI, K)!

The label on the holotypic specimen has the additional data: "abundant, February 1925. The nuts sent although green are fully grown. These nuts are the favourite food of two species of Turtle which abound in the streams where this pandanus grows."

SPECIMENS EXAMINED: Australia, same data as above, but 6 Nov. 1926 (staminate) (BRI); and ditto, 1927 (FI, K).

DISCUSSION: P. de-Lestangii Martelli is a clearly distinct species. The collector, A. de Lestang, was an amateur naturalist who gathered abundant material and recorded good data. Drawing his description and figures from this material, Martelli published this easily recognizable species. He described the drupes as with 1 cell, or 2–3, or rarely 4–5 in one series. His illustrations show 1–2–3-celled drupes in lateral and apical views, and 1–2-celled ones in longitudinal median section. The holotype (FI) has been studied, as well as the abundant isotype (BRI); together these contain 309 drupes that

are 1-celled, 53 of the 2-celled, and 2 of the 3-celled. On the angular shoulders leading to the apex of the broader drupes there are often pale, corky scars, very similar to stigmas, especially if the apex is partly eroded. For instance, when the writer first carefully sorted the drupes of the isotype, he separated 7 as with 3 cells, judged by the apparent stigmas. Later, by sectioning some, and by comparison, it was discovered that 6 of them had the body only 2-lobed and in section 2-celled, 2-seeded. In each case they had two stigmas in a line, and the third spot was actually a corky scar, not a stigma. The single remaining one was truly 3-celled, but it was a shorter, asymmetric, basal one with the three stigmas in a triangle and centripetal.

Count Martelli assigned P. de-Lestangii to section Hombronia, as its only representative on the Australian continent. On the contrary, it is now clear that when the stigmas are 2, they are in line but centripetally directed, flush, and elliptic to obovate or suborbicular. When 3, the stigmas are centripetal. In true Hombronia the several stigmas are arranged in a line or in several parallel lines, with the stigmas like flaps or teeth directed laterally at right angles to the line of carpels. In structure the fruits of P. de-Lestangii are quite at variance with this section. The species is here reassigned to the section Microstigma.

A. de Lestang in later observations (in litt. ad W. D. Francis, 30/9/42) stated that the species succeeds well in cultivation as an ornamental or for hedges, even in dry ground. "In the wild state thrives in bog and shallow water, loving best the fringe of deep pools where it anchor[s] itself with props extending to the bottom of the deepest water. In spring displays long spikes of yellowish flowers, male sessile, . . ." On his staminate sheet is his letter with many details, including: "Each grown tree blooms late in October and early November carrying one or two male inflorescences but only the older trees bear syncarps rarely more than two. Both male flowers and syncarps grow simultaneously on neighbouring limbs, and the specimens forwarded were from one tree."—He seems to state that the trees are monoecious, but no such species is known. It is quite possible that he observed interlacing branches from adjacent staminate and pistillate plants. Until

proven to the contrary, it will be assumed that this species is dioecious, like all other known species of *Pandanus*.

He continues: "When a syncarp is fully grown (if allowed) although still green, the balloon-like oval-shaped stem shrinks to nothing within a few days, as soon as the stem [or core] begins to shrink the drupes fall down, slipping in a bunch.

"Thousands of White Cockatoos (*Cacatua galerita*) systematically comb the *Pandanus* for syncarps, beginning in February, they tear down each drupe in quest of a kind of fly larvae which, I think, are solely associated with this fruit. The greater part of the drupes fall in the water below where herds of turtles gluttonously swallow whole the falling drupes; those falling upon the banks are not lost either, for when all the *Pandanus* are clean of syncarps the cockatoos search the ground carefully for the dry nuts and with their powerful beak crush and extract the edible parts."

Consideration must be given to *P. aquaticus* F. Muell., which in 1856 was published as a provisional name, but in 1865 and 1874 was validated as a species. In these accounts von Mueller stated that the plant lacked aerial roots, was smaller and more slender, and had separate drupes. He gave no locality and cited no specimens. Legally *P. aquaticus* F. Muell. is valid. The holotype in Melbourne was studied in 1958. It is a single leaf 79 cm long, 3.7 cm wide. It was collected in December 1855 on the Upper Victoria River, labeled with the name von Mueller, but probably was collected by Leichhardt. No fruit was preserved. An isotype of this was sent to Kew, and Solms stated (Linnaea 42:69, 1878) that it was staminate. Warburg listed it (Engler's Pflanzenreich IV, 9:85, 1900) with the "Species incertae sedis," and could neither supplement the description nor cite additional collections. S. T. Blake (Austral. J. Bot. 2:131, 1954) reviews the history of von Mueller's several publications of *P. aquaticus* and concludes correctly that his "remarks given are sufficient to validate the name." He reduces *P. de-Lestangii* Martelli to its synonymy, believing that there is but a single *Pandanus* species with unicellular drupes in the area of northern Northern Territory and northwest Queensland.

The present writer is in full sympathy with efforts to document and establish the identity of early described species. However, in this case, *P. aquaticus* F. Muell. rests upon a few non-diagnostic, descriptive words, and upon one leaf and a staminate inflorescence. It seems best treated as a valid name for a species so incompletely known that it should be left a species dubia, particularly as it is not safe to assume that only a single species of *Pandanus* can grow in one area. The next name, *P. de-Lestangii* Martelli, was based on good material from near Burketown, Queensland, and was published with an excellent diagnosis and illustration. This name is here adopted.

Pandanus adscendens sp. nov. (sect. *Pandanus*)

Fig. 242

DIAGNOSIS HOLOTYPI: Arbor 7 m alta 18 cm diametro, cortice tuberculosa, radicibus fulturosis 1–1.5 m longis 4 cm diametro verruculosis, foliis 1.3–1.6 m longis proxima basem 7 cm latis in media 5.5 cm latis coriaceis in sectione oblate sinuose M-formatis gladiformatis ex basi in apice subulato diminuentibus (apice non preservato) basi amplexicauli et inermi, ex 6–9 cm marginibus cum aculeis 1.8–3 mm longis 3–11 mm separatis crassiter subulatis adscendentibus brunneis vel cum apicibus brunneis, midnervo infra ex 15–20 cm cum aculeis 1.6–2.2 mm longis 13–45 mm separatis graciliter subulatis adscendentibus, in sectione mediali marginibus cum subulato-serris 1–2 mm longis 4–10 mm separatis, midnervo infra cum serris simulantibus sed 10–32 mm separatis, proxima apicem marginibus et midnervo infra cum subulato-serrulis 0.2–0.7 mm longis 2–7 mm separatis, pedunculo 13 cm longo bracteato, syncarpio solitario, nucleo 13 cm longo 4.5 cm diametro cylindrico-ellipsoideo obtuse deltoideo, phalangibus 5–5.6 cm longis 3.3–4.2 cm latis aurantiaco-luteis crassiter pyriformatis vel cuneato-pyriformatis apice rotundato (rariter subtruncato) parte $\frac{2}{5}$ supera libera, suturis lateralibus per $\frac{1}{2}$–1 parte libera distinctis 4–7-angulosis lateribus lateralibus laevibus lucidis in sicco palliditer brunneis subcurvatis vel planis, sinibus centralibus apicalibus
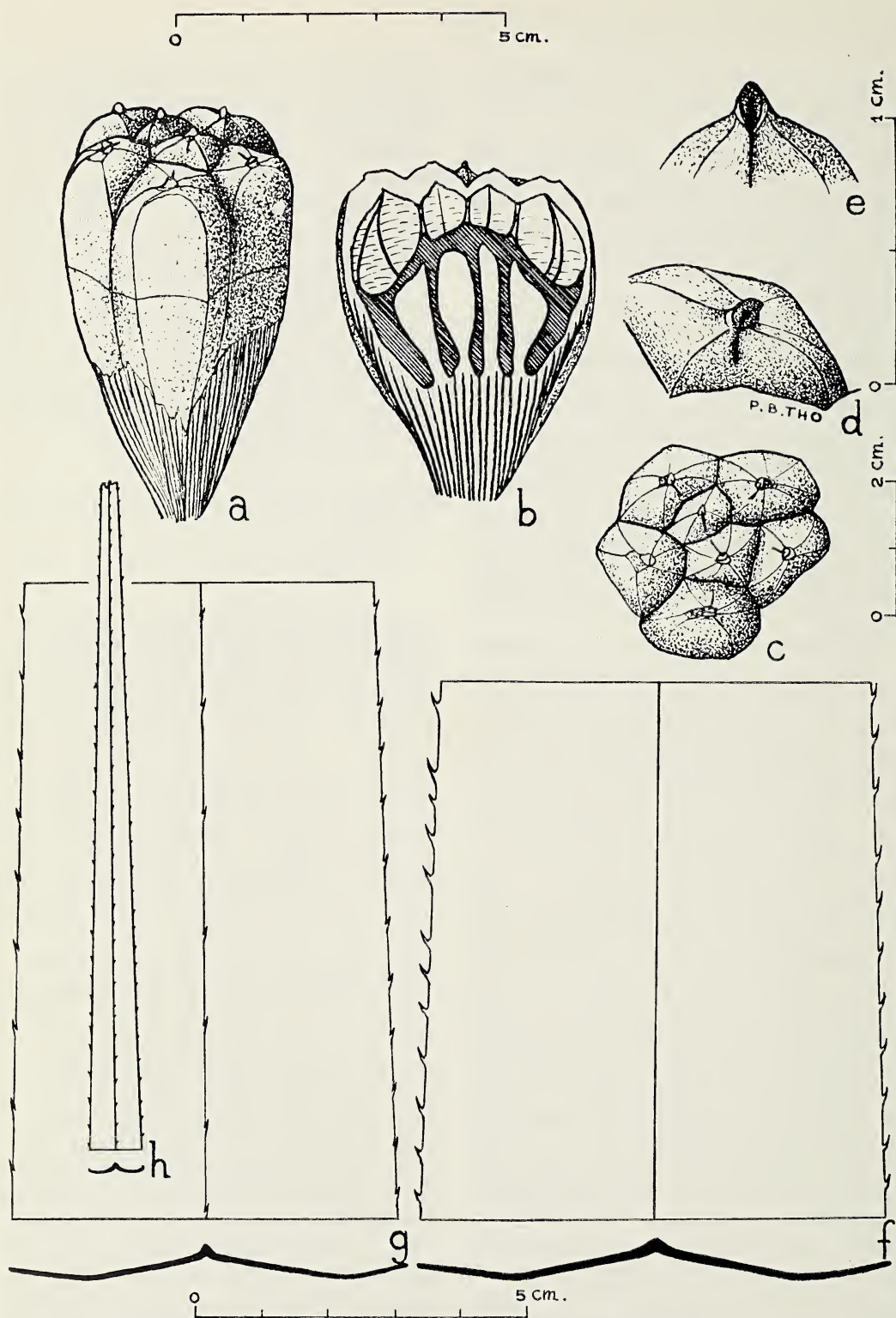
Fig. 242. *Pandanus adscendens* St. John, from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* apex of marginal carpel, oblique view, × 4; *e,* apex of central carpel, oblique view, × 4; *f,* leaf base, lower side, × 1; *g,* leaf middle, lower side, × 1; *h,* leaf apex, lower side, × 1.

3–6 mm profundis V-formatis, carpellis 6–11 apicibus centralibus minoribus rotundato-pyramidalibus vel suboblato-pyramidalibus illis marginalibus valde oblato-pyramidalibus vel semiorbicularibus et plerumque cum cavite parvo distali omnibus adscendentibus vel paucis divergentibus, stigmatibus 1–1.5 mm longis apicalibus ovalibus vel orbicularibus obscuris sulcatis obliquis centripetalibus, sinibus proximalibus profundis ½–⅔ ad fondam extentis, endocarpio supramediali 2–2.2 cm longo osseoso obscure brunneo lateribus lateralibus 3–4 mm crassis, seminibus 12–15 mm longis ellipsoideis vel obliquiter ellipsoideis, mesocarpio in apice quaeque carpellae cavernam cum fibris fortibus longitudinalibus paucis et membranis medullosis formanti, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 7 m tall, 18 cm in diameter; bark with prominent tubercles or warts; prop roots 1–1.5 m long, 4 cm in diameter, warty; leaves 1.3–1.6 m long, 5–7 cm wide near the base, 3.6–5.5 cm wide at the middle, coriaceous, in section depressed sinuous M-shaped, sword-shaped, tapering from the base to the subulate apex, but the actual tip not preserved, the very base amplexicaul and unarmed, but at 6–9 cm the margins with prickles 1.8–3 mm long, 3–11 mm apart, heavy subulate, ascending, brown or brown-tipped; the midrib below beginning at 15–20 cm up with prickles 1.6–2.2 mm long, 13–45 mm apart, slender subulate, ascending; at the midsection the margin with subulate-serrae 1–2 mm long, 4–10 mm apart; those of the midrib below similar but 10–32 mm apart; near the apex the margins and midrib below with subulate-serrulations 0.2–0.7 mm long, 2–7 mm apart; peduncle 13 cm long, bracted; syncarp solitary, the core 13 cm long, 4.5 cm in diameter, cylindric-ellipsoid, obtusely deltoid; phalanges 4.8–5.6 cm long, 2.5–4.7 cm wide, 2.3–4.1 cm thick, orange-yellow, pyriform or cuneate-pyriform, the apex rounded (rarely flattish), upper ⅖ free and in the free part the lateral sutures distinct from half to all its length, 4–7-angled, the sides smooth, shining, when dried light brown, gently curving or plane; apical central sinuses 3–6 mm deep, V-shaped;

carpels 6–13, the central apices somewhat the smaller, pyramidal or slightly oblate pyramidal to semiorbicular and most of them with a small distal concavity, the tips ascending or on a few slightly divergent; stigmas 1–2 mm long, apical, oval to orbicular, dark, creased, oblique, centripetal; proximal sinus deep, running ½–⅔ way to valley bottom; endocarp supramedian, 2–2.2 cm long, bony, dark brown, the lateral walls 3–4 mm thick; seeds 12–15 mm long, ellipsoid or obliquely so; apical mesocarp in each carpel forming a cavern with a few strong longitudinal fibers and white medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, Queensland, Green Island, off Cairns, beach forest with *Erythrina, Cordia subcordata, Morinda citrifolia,* Feb. 9, 1958, *H. St. John 26,266* (BISH).

Fig. 243*a*. *Pandanus darwinensis* St. John, from holotype. Habit of mature trees.

FIG. 243b.   *Pandanus darwinensis* St. John, from holotype. Young trees and a detached syncarp.

SPECIMENS EXAMINED: Australia, Queensland, Green Island, off Cairns, beach forest with *Erythrina, Cordia subcordata, Morinda citrifolia,* Feb. 9, 1958, *H. St. John 26,269* (BISH); Percy I., Dec. 1870, *McGeorge* (MEL); South Brooke I., *G. Tandy* (A); cult., Botanic Garden (Brisbane), *C. T. White 3,332* (A).

DISCUSSION: *P. adscendens* is a member of the section *Pandanus,* as is its closest relative *P. Blakei* St. John, also of Green I., a species with the phalanges with the central apical sinuses 1.5–3 mm deep; carpels 9–12; prop roots sparingly muriculate; leaves 8–8.5 cm wide, and the midrib below unarmed to beyond the middle. *P. adscendens* has the phalanges with the central apical sinuses 3–6 mm deep; carpels 6–13; prop roots warty; leaves 5–7 cm wide, and the midrib below beginning at 15–20 cm up with ascending slender subulate prickles 1.6–2.2 mm long, and 13–45 mm apart.

The new epithet is the Latin participle *adscendens,* ascending, and is given with reference to the direction of the lower spines of the leaves.

Pandanus darwinensis St. John (sect. *Pandanus*)

Fig. 243 *a, b*

An isotype of this species is found in the collections of Martelli in Firenze. With it is a letter from the collector, C. E. F. Allen, Superintendent of Agriculture, Darwin, Northern Territory, Australia, and two excellent photographs. These are reproduced here by permission of the Istituto Botanico, Firenze. From them the following additional details of description can be derived.

EXPANDED DIAGNOSIS: Trees up to 6 m in height; trunk erect, simple, at length forking into erect branches; prop roots, if any, short; bark rather smooth; leaves ascending, then spreading, not becoming bent; infructescence with a single syncarp; peduncle about 63 cm long, recurving; syncarp 28 cm long, 21 cm in diameter, wide ellipsoid, bearing about 26 phalanges.

The type locality is near Darwin, Northern Territory, and the photographs reveal that the species is littoral on marine shores.

Revision of the Genus *Pandanus* Stickman, Part 24
Seychellea, a New Section from the Seychelles Islands

HAROLD ST. JOHN[1]

Seychellea sect. nov. (subgen. *Pandanus*)

CARPELLIS BINIS CONNATIS, stigmatibus binis arcuatis in lateribus oppositis cavitonis terminali affixis, cavo cum stigmatibus falsis cordatis multis, dissepimento lato toto ex fibris longitudinalibus distinctis multis formatis. Arbor cum syncarpiis grandibus sphaericis.

Carpels 2, connate throughout; stimas 2, like slender arcs on opposite sides of the terminal cavity which is filled with many elevated, cordate, unequal structures that imitate stigmas; dissepiment with a pale, thin, cartilaginous tissue next to each seed, then all the rest of the broad interior solely of many, strong, separate, longitudinal fibers. Tree with large spherical syncarps.

HOLOTYPUS: *Pandanus Hornei* Balf. f., in Baker, Fl. Mauritius and Seychelles 397, 1877.

This species, when described, was not placed in a section. Later it was assigned to section *Vinsonia* by Warburg (Pflanzenreich IV, 9:54, 57, 1900), and with this placement Martelli concurred (Webbia 4(1):94, 1913). In his redefinition of the sections, the present writer placed it in section *Dauphinensia* (Pacific Sci. 15(3):341, 1961). He now removes it from there and makes it the type of a new section. Like the Madagascar species of section *Martellidendron,* it is remarkable for having the dissepiment between the seed cavities formed not of a solid, bony tissue, but of a mass of distinct, longitudinal fibers. Also the two arclike stigmas, on opposite edges of the apical disc or concavity, are very similar.

As for differences, the section *Martellidendron,* with 4 species from Madagascar, has the dissepiment solely of loose, longitudinal fibers; the phalange apex truncate, with an elliptic, firm disc, divided into quarters by deep valleys; the 2 stigmas lateral on opposite sides of the disc. The section *Seychellea* has the dissepiment of pale, thin, cartilaginous tissue next to each seed face, then all the rest of its broad interior made solely of many strong, separate, longitudinal fibers; the 2 arclike or parenthesis-like stigmas lateral on opposite sides of the rim of the apical cavity which is filled with many cordate pseudo-stigmas.

Judging by Martelli's illustration (Webbia 4(1):t. 16, fig. 2, 1913) the fruit would be a 1-celled drupe. His specimen has been examined. He had a whole syncarp, but sectioned only one phalange. He made the cut between the two stigmas, just shaving the fibrous dissepiment, and cleaving only one of the two seed cavities. That the other seed cavity is there can be told by pushing a needle through the fibrous dissepiment. The phalanges seem to be always 2-celled. A new drawing is presented here to bring out the diagnostic structure of the dissepiment.
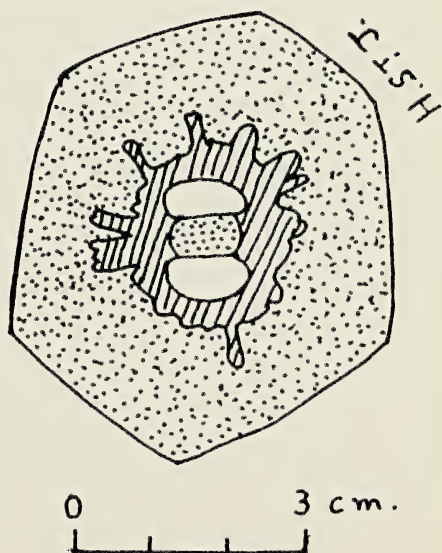
FIG. 244. *Pandanus Hornei* Balf. f. in Baker. Transverse section of phalange, showing fibrous septum, two seed cavities, endocarp, fibrous mesocarp, and exocarp, × 1. Drawn from Isole Seychelles (FI).

[1] B. P. Bishop Museum, Honolulu, Hawaii 96819. Manuscript received March 11, 1963.

Pandanus Hornei Balf. f., in Baker, Fl. Mauritius and Seychelles 397, 1877; Warburg, Pflanzenreich IV, 9:57, 1900; Martelli, Webbia 4(1):17, t. 16, figs. 1–3, 1913; St. John, Pacific Sci. 15(3):341, 345, figs. 20–21, 1961 (sect. *Seychellea*).

Fig. 244

SUPPLEMENTARY DESCRIPTION: Leaves at midsection with 104 parallel secondary veins in each half, the tertiary cross veins visible below toward apex, forming square or short oblong meshes.

SPECIMENS EXAMINED: Isole Seychelles, dal Museo di Parigi (FI).

The new section can be placed in the key to *Pandanus* (Pacific Sci. 14(3):226, 1960), by replacing the first heading R, with the following:

R. Phalange with the septum between the two cells of many loose fibers,

1. Septum wholly of loose fibers; phalange apex an elliptic disc cut by valleys into quarters; stamens umbellate on the capitate apex of the column, and with abortive gynoecium. . . . . *Martellidendron*

1. Septum of a thin cartilaginous tissue next to each seed, then its broad interior solely of loose fibers; phalange apex concave and filled with unequal, cordate pseudo-stigmas. . . *Seychellea*

Revision of the Genus *Pandanus* Stickman, Part 25
Pandanus tectorius var. *sinensis* Warburg

Harold St. John[1]

Pandanus tectorius Warburg var. *sinensis* Warb., Engler's Pflanzenreich IV, 9:48, 1900. (sect. *Pandanus*)

THE ENTIRE PRESENTATION of this variety was: "Folia minora angusta flagello longo terminata, spinis marginalibus quam in typo majoribus armata. Phalanges minores pauci-(5–6–) loculares. Südchina. (Warburg, Naumann, Henry)."

This characterization is wholly inadequate, and no type was indicated. In the Berlin herbarium the original specimens were still to be found in 1962. *Warburg 5,482* from Macao consists of a single leaf 77 cm long, 3 cm wide; near the base the marginal prickles are alternately small and large, the latter 4–6 mm long, straight subulate, stramineous, ascending at 45°, the successive prickles 5–12 mm apart; the subulate leaf apex at the point about 10 cm down 1.5 mm wide. Until complete material is known from Macao, *Warburg 5,482* is undeterminable.

The second specimen was from Hong Kong, Winter, 69/70, *Dr. C. Naumann,* and it contains parts of four leaves. It is probably *P. remotus* St. John.

The third collection is more adequate. It is from Hainan, 1889, *A. Henry.* One sheet bears two young pistillate inflorescences. A second bears a pocket with several very young pha-

langes, and one mature phalange 3.3 cm long, but this is a distorted, very asymmetric, 6-celled, basal one, not suitable for identification, but, since it is the only fruiting one in the series, it is here designated as lectotype of the var. *sinensis.* A third sheet with the same data is *A. Henry 8,290.* This bears parts of two good staminate inflorescences. These three sheets from Hainan represent a plant that differs from *P. hainanensis* St. John in its much broader leaves, etc. These specimens are not complete enough to identify.

In conclusion, the var. *sinensis* Warb. is in two parts indeterminable, and in the third part probably synonymous with *P. remotus* St. John.

Subsequent botanists, apparently content with Warburg's description, have identified numerous collections as belonging to this variety. They have recorded the plant from the Mascarene Islands, India, Cambodia, Malaya, Tonkin, Philippines, Formosa, New Caledonia, Australia, Tonga, and Hawaii. Their collections are diverse, and do not represent one species or variety. Since the original var. *sinensis* Warb. is ill-defined and incapable of identification, these later locality records can be rejected without further comment.

Since the author considers the publication of *P. tectorius* by Parkinson (or Solander) invalid, he now attributes it to Warburg, who in 1900 first validly published the binomial with a description.

[1] B. P. Bishop Museum, Honolulu, Hawaii 96819. Manuscript received March 11, 1963.

Reversal of Ethionine Inhibition by Methionine during Slime Mold Development

HANS R. HOHL AND SUSAN T. HAMAMOTO[1]

Dictyostelium discoideum, a cellular slime mold, has been shown by Filosa (1960) to produce abnormal fruiting bodies when grown on *Escherichia coli* in the presence of 1.2×10^{-3} M ethionine. The fruiting bodies obtained under those conditions were described as short, with thick stalks and elongated sori. At a concentration of 4.8×10^{-3} M no growth occurred. Starting from this initial observation we have attempted to answer the following questions: Which elements of development, such as morphogenesis or differentiation of spores and stalk cells, are affected at various concentrations of ethionine? Which phases of the life cycle are sensitive to ethionine? What is the mechanism of ethionine inhibition? Answers to these questions might possibly provide clues to the mechanism of development in these organisms, where an integrated mass of myxamoebae produces, in the absence of an external source of energy, a well-proportioned fruiting body composed of a cellulose-ensheathed stalk bearing a lobose sorus of spores.

MATERIALS AND METHODS

Myxamoebae of *Dictyostelium discoideum* NC-4(S2), a haploid strain, were grown at 24°C in the presence of *Escherichia coli* B/r on a medium containing 1% lactose, 1% peptone, and 1.5% Difco agar. After 44–46 hours, shortly before the cells reached the stationary growth phase, they were harvested with ice-cold Sörensen's phosphate buffer (0.016 M, pH 6.0), washed, and their concentration adjusted to $1.5–2.0 \times 10^8$ cells/ml. A 0.5-ml sample of cell suspension containing $0.75–1.0 \times 10^8$ cells was spread onto millipore filters

according to the method of Sussman and Lovgren (1965). For this the millipore filters (48 mm diameter, black), resting on absorbent filter pads, were placed in plastic petri dishes (60 mm diameter). Prior to the addition of myxamoebae the pads were soaked with 1.5 ml of phosphate buffer containing per ml 0.67 mg of streptomycin and 0.13 mg of sodiumlaurylsulfate together with appropriate concentrations of the test solution. The sodiumlaurylsulfate appears to contribute to a more uniform development of the population and to enhanced effectiveness of at least some compounds, probably by increasing the cell permeability without having any obvious effect on normal development. All cultures were incubated at 24°C in the dark; in some experiments when the plates were kept at room temperature overnight, the temperature varied between 21° and 25°C. The plates were scored every 4 hours until no further developmental changes were observed. To test the effect of ethionine on growth and agglutination, the cells were grown on *E. coli* in shake cultures in the presence of the compound and the growth curves determined (Hohl and Raper, 1963), or washed cells were incubated in roller tubes and their pattern of agglutination was observed (Hohl and Raper, 1964). For the growth in shake cultures, *D. discoideum* V-12 was used.

RESULTS

Ethionine completely inhibits growth of *Dictyostelium* at a concentration of 3.0×10^{-2} M and shows no inhibitory effect at 1.0×10^{-3} M (Fig. 1). In no concentration, however, does it interfere with agglutination of myxamoebae as judged from the behavior of cells in roller tubes. Even at a concentration of 3.0×10^{-2} M there was no sign of inhibition either in the rate of agglutination or in the size of the agglutinates formed. This indicates that
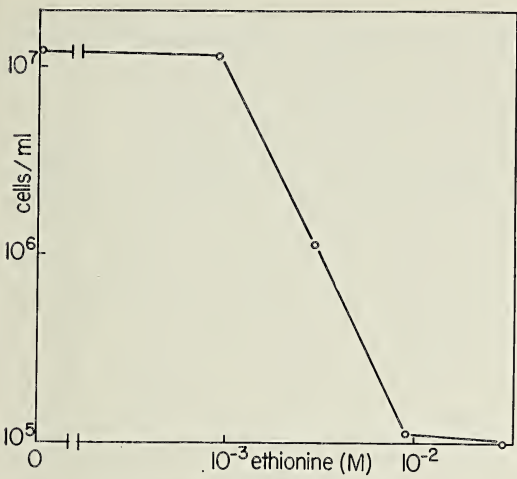
Fig. 1. Growth of *Dictyostelium discoideum* on *Escherichia coli* in the presence of various concentrations of ethionine. The ordinate indicates cells/ml at the end of the growth period (46 hours). The inoculum consisted of 1.0×10^5 myxamoebae/ml.

cell adherence or "stickiness" is not suppressed by ethionine. This result corroborates the experiments to be reported next, where it was found that even high concentrations of ethionine do not completely inhibit streaming and a type of massing of cells reminiscent of aggregation.

In order to test the effect of ethionine on the developmental stages per se, the myxamoebae were grown in the absence of ethionine first and then washed populations were subjected to ethionine as described under materials and methods. Figure 2 presents the effects of various concentrations of ethionine on the development

ETHIONINE CONCENTRATION (M)	DIFFERENTIATION INTO			TYPICAL FORMS	TYPE NO.
	SPORES	SHEATH	STALK CELLS		
0	+	+	+		1
7.5×10^{-4}	+	+	+		2
1.5×10^{-3}	−	+	+		3
3.0×10^{-3}	−	−	+		4
6.0×10^{-3}	−	−	−		5
1.5×10^{-2}	−	−	−		6

Fig. 2. Influence of increasing concentrations of ethionine on the development of *Dictyostelium discoideum*. The results represent the final stages of development regularly reached after 24 to 30 hours.

of *D. discoideum*. Ethionine did not appreciably reduce the viability of the myxamoebae during the time of the experiment. Hence, the effects observed cannot be attributed to a partial killing of the cell population. A concentration of 1.5×10^{-2} M completely inhibits morphogenesis, although some streaming may occur resulting in the formation of vaguely defined clumps that usually disappear within 24 hours. At 6.0×10^{-3} M large, flat mounds of myxamoebae are formed out of which tiny papillae may protrude, rudimentary signs of induction of polarity and fruiting body formation. The large number of these small papillae per mound indicates further that the critical mass, i.e., the mass of cells capable of integrated behavior (Hohl and Raper, 1964), has been drastically reduced. At a concentration of 3.0×10^{-3} M the myxamoebae collect into large aggregates that split up to form many finger-like protrusions. These protrusions are made up typically of a heavy mass of cells at the base, a short, thick stalk-like structure oftentimes carrying at its apical end a lobose mass of cells somewhat resembling a sorus. Up to this stage all the structures are made up of roundish cells without signs of spore differentiation or production of a cellulose sheath. Some large vacuolated cells, however, are present and we interpret them as representing stalk cells. At a concentration of 1.5×10^{-3} M stalks are formed and are ensheathed in a smooth cellulose envelope. The outside of the sheath is often covered with masses of undifferentiated cells, thus making the structures as a whole appear distorted. No spores are found in these fruiting bodies, but clumps of undifferentiated cells may occur at the tip of the stalk. Because of the still heavy base and the stalk without sorus the whole structure at this level often resembles a bowling pin. At a concentration of 7.5×10^{-4} M the fruiting bodies, apart from occasional distorted forms, are normal in appearance though reduced in size. No apparent effect can be observed at lower levels of ethionine. For convenience the different levels of inhibition have been numbered from 1 to 6, as indicated in Figure 2. In general, spore differentiation is most sensitive to ethionine, followed by sheath production, stalk cell differentiation, and lastly morphogenetic move-

ment. Of developmental stages, spore formation is also the most sensitive to treatment with 2-mercaptoethanol, as shown by Gerisch (1961). Spore formation and normal morphogenesis are closely linked, as spores have been found only in normal sori, and normal-appearing sori always contained spores.

Whereas no morphogenesis takes place in the presence of 1.5×10^{-2} M ethionine, the simultaneous addition of methionine in increasing amounts leads to the formation of progressively more normal appearing fruiting bodies (Fig. 3). The structure of the resulting sorocarps follows the same pattern as described above for ethionine-treated populations. When the concentration of methionine approaches twice that of ethionine the fruiting bodies look normal but are somewhat smaller in size (equal to stage 2) compared with controls growing on methionine alone or on the buffer alone. If the experiment is repeated with 1/5 the concentration of ethionine and a correspondingly lowered amount of methionine the results remain unchanged. This demonstrates that the ratio of ethionine to methionine is the critical factor, rather than the absolute amounts of either compound. Ethionine clearly behaves like a competitive inhibitor of methionine.

Next, ethionine sensitivity at the various developmental stages (after cessation of vegetative growth) was determined. For this, populations were exposed to 1.5×10^{-2} M ethionine at selected points in their development for various periods of time. Some of the results are sum-
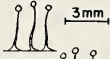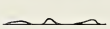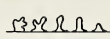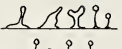
FIG. 4. Sensitivity of various stages of slime mold development to the inhibitory action of ethionine. The time scale indicates hours after deposition of the washed myxamoebae populations together with the onset of aggregation (*ag*), migration (*mig*), and culmination (*cul*) of the control population. *Solid lines* denote the presence of ethionine, *dotted lines* of methionine. The resulting types of sorocarps are numbered according to Figure 1. They represent the final levels of development reached under the respective conditions. The delay in time to reach these final stages with respect to the controls is approximately equal to the time the populations were exposed to ethionine.

marized in Figure 4. Before and after the treatment with ethionine the cells were kept on equimolar concentrations of methionine. This was done in order to assure a quick removal of any possible free ethionine in the internal amino acid pool (Wright and Anderson, 1960) that might obscure the results. In fact, it was found that when the cells were transferred (after treatment with ethionine) to buffer alone, instead of to buffer plus methionine, morphogenesis was permanently inhibited. This strongly indicates the presence of a rather large internal pool where the ethionine can persist for hours, unless it is exchanged for exogenous methionine. The main conclusions to be drawn from Figure 4 are: (1) the entire morphogenetic part of the life cycle up to the actual formation of the stalk is sensitive to ethionine, and (2) the inhibitory effect of ethionine is a gradual one, the damage becoming more severe the longer the cells are in contact with the substance. An important point is that even if ethionine is administered just prior to commencement of stalk production the inhibitory

FIG. 3. Influence of ethionine and methionine, alone and in combination, on the development of *Dictyostelium discoideum*. The results represent the final stages of development regularly reached after 24 to 30 hours.

effect is still very strong. Once the stalk is being formed the mass rises above the substrate and the further effects of ethionine are difficult to assess since the substances in the filter pad are no longer in direct contact with the cell mass. If ethionine is added for a certain period of time before aggregation, aggregation itself is also disturbed as described previously, i.e., only vaguely defined clumps form as the result of some streaming, or there is no reaction at all. Also, if ethionine is added after aggregation, then the proper polarization of the aggregated mass is disturbed and many small tips are formed as long as the contact with ethionine is maintained. The results of this experiment show that ethionine acts on several phases of the developmental sequence as well as on the vegetative growth. Most significantly, however, it acts directly on the last stage, culmination.

DISCUSSION

Ethionine interferes with various stages of the life cycle of *Dictyostelium,* such as vegetative growth, aggregation, and culmination. We have been able to show that the inhibition of the later stages of development is not necessarily a consequence of inhibition of earlier ones, since addition of ethionine as late as just prior to culmination is still inhibitory to a large extent.

Spore differentiation is most sensitive to the action of ethionine, followed by cellulose sheath formation, stalk cell differentiation, and finally, morphogenetic movement. A similar sequence of sensitivity has been observed by Gerisch (1961) in the case of mercaptoethanol. Ethionine, then, seems to be primarily an inhibitor of differentiation. In turn, several aspects of disturbed morphogenesis, such as lack of a sorus or production of a short bulky stalk, can be indirectly attributed to this effect. Moreover, how can the cell mass build a slender, evenly tapered stalk in the absence of any cellulose component for structural support?

We have established that ethionine acts as a competitive inhibitor of methionine. This conclusion is based on the observations that (1) methionine is able to reverse the inhibitory effect of ethionine when the two are added to the cultures simultaneously, and (2) the final product of development is a function of the ratio of the two components rather than of their absolute amounts. The proteins incorporating ethionine instead of methionine are rendered biologically inactive and, therefore, normal development cannot proceed. It may be imagined that the various disturbances effected by ethionine have a common cause, but this is unlikely since ethionine is probably incorporated into a variety of proteins normally containing methionine. One point deserves mentioning: the ethionine has to be in contact with the cell population for at least 4–8 hours to produce any persisting inhibitory effect. At least two possible explanations might account for this: (1) ethionine slows down protein synthesis as long as it is in contact with the cells, so that only a small amount of ethionine-containing material is formed; and (2) the protein turnover is high, so that the ethionine-containing proteins are rapidly broken down and replaced by the normal methionine-containing ones, as soon as the cells are switched from ethionine to methionine.

The fate of the ethionine in the cell population has not been directly traced. However, from the work of Wright and Anderson (1960) on methionine metabolism in *Dictyostelium* we are able to get some information directly applicable to our situation. These authors have shown that the endogenous "free" amino acid pool is a function of the stage of development only and is not influenced by exogenous methionine. However, exogenous methionine can exchange with endogenous methionine, and the extent of this exchange is a linear function of the exogenous methionine present. This means that increasing the external methionine concentration does not alter the size of the internal pool, but does increase the rate of exchange between exogenous and endogenous methionine. If we assume that ethionine behaves similarly in this respect, it then becomes clear that increasing the amount of ethionine in the medium does not simply add more ethionine to the existing endogenous amino acid pool, but results in a higher exchange of ethionine for methionine between this pool and the environment. In this way we have changed the ratio of methionine to ethionine, which is the essen-

tial determinant for subsequent developmental events.

The effectiveness of ethionine up to the point of actual stalk formation indicates that at least some of the proteins essential for normal development are formed right up to the point of culmination. Wright and Anderson (1960) have shown that certain ethanol-insoluble, methionine-containing proteins are produced at an increased rate during the stage of pre-culmination. It will be of interest to determine whether these proteins are enzymes involved in cellulose synthesis or if they are structural proteins responsible for cell polarization and differentiation. Evidence from experiments with colchicine in conjunction with electron microscopy indicates the occurrence of such a proteinaceous cytoskeleton in *Dictyostelium* (Hohl and George, 1966).

SUMMARY

Ethionine progressively inhibits the development of *Dictyostelium discoideum,* from a concentration of 7.5×10^{-4} M (which induces somewhat smaller but normal fruiting bodies) to a concentration of 1.5×10^{-2} M (which results in complete inhibition). Intermediate concentrations produce a variety of distorted forms. With increasing concentrations the inhibitory effect is first noticed in spore differentiation, then in cellulose sheath production, followed by stalk cell differentiation, and finally in morphogenetic movement.

Simultaneous addition of methionine reverses the effect of ethionine, the final result depending on the ratio of ethionine to methionine rather than on the absolute amounts of either substance administered. Ethionine exerts its effect at any time in the life cycle up to the actual formation of the stalk, the final appearance of the fruiting bodies being a function
both of the stage at which the ethionine was applied and of the period of time the cultures were in contact with it. The results indicate that, first, ethionine acts as a competitive inhibitor of methionine, and, second, the protein or proteins incorporating ethionine and thereby rendered biologically inactive are being produced continuously up to the time of actual stalk formation.

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Comparative Decay Resistance of Twenty-five Fijian Timber Species in Accelerated Laboratory Tests

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ABSTRACT: Specimens from the heartwood of 2–5 trees of each of 25 species of Fijian rain forest timbers were tested by the laboratory soil-block method against two white-rot fungi, *Fomes lividus* (Kalch.) Sacc. and *Pycnoporus coccineus* (Fr.) Bond. and Sing., syn. *Coriolus sanguineus* (L. ex Fr.) G. H. Cunn.; and against two brown-rot fungi, *Lenzites trabea* Pers. ex Fr. and *Coniophora olivacea* (Fr.) Karst. The species most resistant to decay were *Palaquium hornei, Intsia bijuga, Fagraea gracilipes, Syzygium* spp. complex, and *Dacrydium elatum*. Most of the species tested were highly susceptible to decay.

There was a tendency, both among species and within species, for the denser and less water-absorbent wood to be more resistant to decay. Also, the outer heartwood was, in general, more resistant to decay than inner heartwood.

A RECENT STUDY was made of the decay resistance of a number of tropical rain forest timbers of New Guinea (Da Costa and Osborne, 1967). Prior to this there was almost no information on the durability of the rain forest species of New Guinea, or of the East Asian and South Pacific areas in general. Because more and more local timber is now being used in these countries, there is an increasing need for knowledge of the approximate durability of these timber species so that efficient use can be made of the timber available. This situation applies in Fiji, as local timber has not previously been used extensively for permanent structures, and little is known of its performance in service. Unfortunately, although both New Guinea and Fiji have tropical rain forest vegetation, it appears that there are very few species common to both countries, so that information obtained for New Guinea species has little application in the use of Fijian timbers. This fact is a reflection of the great variety of tropical rain forest timbers in the world and emphasizes the need for information on the durability of this large group of timbers.

It is therefore desirable to study the decay resistance of the species occurring most commonly in Fiji so that suitable timber can be selected for a particular use. For example, it is desirable to use the most durable timbers for conditions of high decay hazard, such as for transmission poles, fence posts, sleepers, and bridge timbers. Less durable timbers may be suitable for external joinery, etc., that is, not in ground contact, whereas highly susceptible ones would be unsuitable for any external use in the humid climate without preservative treatment.

One method of obtaining this information is by graveyard stake tests, and a few species are being studied in Fiji in this way (Alston, 1966). However, as these tests take some years to complete, an accelerated laboratory decay test was considered desirable.

MATERIALS AND METHODS

The methods used in this investigation follow closely those used in the study of 26 New Guinea timbers (Da Costa and Osborne, 1967) to which the reader is referred for more detailed information.

Selection of Material

The 25 Fijian timber species examined for decay resistance in these laboratory tests are listed in Table 1, together with local and family names. Although *Swietenia macrophylla* and *Eucalyptus citriodora* are not native to Fiji,

TABLE 1

TIMBER SPECIES TESTED

TIMBER SPECIES	TRADE NAME	FAMILY
Agathis vitiensis (Seem.) Drake	dakua makadre	Araucariaceae
Alphitonia zizyphoides (Spreng.) A. Gray	doi	Rhamnaceae
Calophyllum spp.*	damanu	Guttiferae
Canarium spp.*	kaunicina, kaunigai	Burseraceae
Casuarina nodiflora Forst.*	velau	Casuarinaceae
Dacrydium elatum Wall.	yaka	Podocarpaceae
Endospermum macrophyllum (Muell. Arg.) Pax et Hoffm.	kauvula	Euphorbiaceae
Eucalyptus citriodora Hook.	lemon scented gum	Myrtaceae
Fagraea gracilipes A. Gray	buabua	Loganiaceae
Garcinia myrtifolia A. C. Smith	laubu	Guttiferae
Gonystylus punctatus A. C. Smith	mavota	Gonystylaceae
Heritiera ornithocephala Kosterm.	rosarosa	Sterculiaceae
Intsia bijuga (Colebr.) O. Kuntze	vesi	Leguminosae
Myristica spp.*	kaudamu	Myristicaceae
Palaquium fidjiense Pierre*	bauvudi	Sapotaceae
Palaquium hornei (Hartog ex Baker) Dubard	sacau	Sapotaceae
Parinari insularum A. Gray	sa	Rosaceae
Podocarpus javanica (Burm. f.) Merr.	aumunu	Podocarpaceae
Podocarpus neriifolius D. Don	kuasi	Podocarpaceae
Podocarpus vitiensis Seem.	dakua salusalu	Podocarpaceae
Serianthes myriadenia Planch.	vaivai-ni-veikau	Leguminosae
Swietenia macrophylla King	mahogany	Meliaceae
Syzygium spp. complex*	yasiyasi	Myrtaceae
Terminalia catappa L.	tivi	Combretaceae
Trichospermum richii (A. Gray) Seem.	mako	Tiliaceae
Eucalyptus microcorys F. Muell.[†]	tallowwood	Myrtaceae
Eucalyptus obliqua L'Herit.[†]	messmate	Myrtaceae
Pinus radiata D. Don[†]	radiata pine	Pinaceae
Pseudotsuga menziesii (Mirb.) Franco[†]	Douglas fir	Pinaceae
Tectona grandis L.f.[†]	teak	Verbenaceae

[*] Groups consisting of more than one botanical species but regarded as one commercial species.
[†] Reference timbers of known durability included for comparison.

they have been listed with the other species, as they have been grown in plantations in Fiji for some years.

Timber was collected in Fiji for each species, but often after testing had begun subsequent examination of botanical material showed that there were more than one botanical species within the "species" collected, two or more genera sometimes being represented. Wherever these species have been found to be very similar in appearance in the field, in anatomical structure, physical and strength properties, and durability, the mixture has been regarded as one commercial species. These species mixtures are indicated in Table 1 and are discussed further under "Results." In cases where a species

differed appreciably from the main species of the group, it has been omitted.

As these decay tests give comparative results only, five reference timbers, whose durability and performance in service are well known and which represent a wide range of durability, were included and are also listed in Table 1.

As a general rule, specimens from five separate trees were tested for each timber species. However, this number was not always available and smaller numbers of trees were sampled for a few species (see Table 2). The timber was shipped in the form of green logs, and then a pith-to-bark billet measuring approximately 24 inches longitudinally and 6 inches tangentially was cut from each tree, the

TABLE 2

PROPERTIES AND DECAY RESISTANCE OF SPECIES TESTED*

| TIMBER SPECIES | NO. OF TREES | WOOD PROPERTIES | | PERCENTAGE WEIGHT LOSS** CAUSED BY TEST FUNGUS | | | |
		Basic Density (lb/cu ft)	Water Uptake (%)	Fomes lividus	Pycnoporus coccineus	Lenzites trabea	Coniophora olivacea
Palaquium hornei	4	54.5 51.0–57.0	22.4 21.4–23.7	0.5 0.2–0.9	0.2 —0.1–0.8	—0.1 —0.2–0.0	0.1 —0.1–0.2
Eucalyptus microcorys†	5	54.0 52.2–56.3	19.2 18.5–20.1	0.6 0.3–0.9	1.2 0.5–2.0	0.2 0.0–0.6	0.5 —3.2–3.8
Intsia bijuga	4	46.0 43.0–50.8	28.3 23.6–31.4	2.4 0.0–8.1	0.2 0.0–0.4	0.0 0.0–0.2	0.2 0.0–0.4
Fagraea gracilipes	2	50.8 49.1–51.9	17.5 17.3–17.8	0.9 0.7–1.2	1.2 0.7–1.7	1.6 1.1–2.2	1.8 0.3–4.0
Tectona grandis†	5	35.7 31.0–38.6	24.9 19.6–31.3	2.6 0.2–6.1	2.0 0.4–5.3	1.2 0.4–3.0	0.3 0.0–1.0
Syzygium spp.	15	47.7 39.4–55.1	22.5 18.8–34.1	6.3 0.2–24.3	3.1 —0.1–21.9	0.6 —0.3–8.7	5.7 —0.2–29.2
Eucalyptus obliqua†	5	38.3 35.3–43.6	38.1 30.7–43.3	9.2 2.1–18.2	1.5 0.4–2.6	0.1 —0.5–0.7	14.9 0.4–23.6
Dacrydium elatum	3	34.5 31.2–38.2	46.9 35.8–84.7	6.2 0.6–16.0	10.1 3.3–20.1	1.8 —0.5–8.2	8.3 —0.3–22.6
Podocarpus neriifolius	4	32.5 29.3–35.9	43.1 30.5–53.8	4.4 1.3–8.3	1.0 —0.2–4.5	7.8 0.0–13.9	16.6 4.3–22.5
Garcinia myrtifolia	5	41.9 37.3–46.2	39.2 35.8–46.6	13.2 2.1–29.9	8.8 0.9–27.5	1.9 0.4–6.3	6.9 0.4–39.6
Heritiera ornithocephala	5	43.1 33.2–50.4	32.8 23.0–51.0	13.9 4.2–28.9	9.0 2.3–27.0	2.3 0.4–6.8	6.3 0.0–17.5
Swietenia macrophylla	5	27.8 24.3–29.6	38.5 33.5–43.0	19.5 13.8–25.6	5.4 —0.2–12.7	2.6 —0.2–10.6	5.1 —0.2–13.0
Palaquium fidjiense	5	25.9 20.9–29.4	56.3 46.1–67.0	15.7 2.8–28.1	10.0 0.6–24.3	2.7 —0.3–14.5	6.3 —0.3–28.4
Serianthes myriadenia	5	26.8 22.3–30.2	46.3 39.8–54.9	26.0 10.0–50.1	9.1 1.2–19.4	6.3 0.6–21.6	14.1 1.0–35.2
Pseudotsuga menziesii†	5	26.0 23.0–28.0	41.5 35.0–48.5	10.6 6.4–16.5	4.4 1.4–12.4	19.0 14.3–25.5	32.2 27.0–37.0
Calophyllum spp.	5	31.9 23.5–38.6	46.2 33.8–65.2	22.6 9.6–35.2	14.2 2.0–27.3	8.7 0.5–25.9	21.4 —0.7–41.0
Casuarina nodiflora	4	52.9 51.0–54.0	31.8 24.6–40.4	19.7 13.6–26.8	26.5 14.4–39.4	5.1 —0.5–9.1	18.2 5.9–28.3
Eucalyptus citriodora	4	41.5 30.8–57.3	42.4 21.6–71.2	24.4 4.4–42.5	27.9 2.8–63.6	7.8 0.5–18.9	18.6 1.2–36.4
Podocarpus vitiensis	5	24.2 22.6–25.7	72.2 44.4–99.5	13.3 8.9–18.8	21.2 14.7–28.0	17.8 8.2–21.3	27.8 23.6–31.0
Alphitonia zizyphoides	2	32.6 30.3–34.8	43.4 39.3–50.6	32.9 28.5–41.8	33.8 28.1–39.7	10.3 6.2–12.7	10.6 0.0–25.6
Agathis vitiensis	5	29.0 26.1–32.9	73.0 41.8–122.6	21.5 16.6–25.1	24.0 15.0–28.4	28.7 17.9–35.3	27.0 18.5–34.3
Parinari insularum	5	38.8 34.0–43.7	51.7 42.0–62.1	29.6 19.6–41.3	31.7 20.3–40.6	16.9 9.2–25.8	27.4 21.7–30.1
Terminalia catappa	4	25.1 16.9–32.8	57.0 43.8–67.7	40.6 28.7–58.1	32.6 24.0–43.5	17.2 4.7–26.3	25.0 10.8–34.3

TABLE 2 (*continued*)

| TIMBER SPECIES | NO. OF TREES | WOOD PROPERTIES | | PERCENTAGE WEIGHT LOSS** CAUSED BY TEST FUNGUS | | | |
		Basic Density (lb/cu ft)	Water Uptake (%)	Fomes lividus	Pycnoporus coccineus	Lenzites trabea	Coniophora olivacea
Gonystylus punctatus	4	**35.3** 29.9–41.6	**54.4** 48.4–60.4	**29.3** 25.1–33.9	**32.0** 23.1–37.7	**28.6** 19.8–38.6	**31.0** 25.0–36.7
Podocarpus javanica	3	**27.7** 24.8–28.8	**103.5** 39.0–149.2	**22.0** 18.5–25.2	**32.0** 28.4–37.0	**35.8** 24.9–44.5	**31.3** 27.0–34.9
Pinus radiata† (sapwood)	5	**28.8** 25.6–32.3	**80.4** 75.3–84.9	**23.7** 21.4–27.5	**27.2** 20.8–36.0	**33.1** 24.4–39.7	**39.7** 38.2–41.0
Canarium spp.	5	**29.4** 26.1–33.8	**49.7** 35.0–77.4	**48.0** 32.1–60.1	**28.9** 21.0–47.4	**24.7** 9.9–35.6	**30.4** 17.4–40.0
Endospermum macrophyllum	5	**25.1** 18.1–29.5	**65.0** 52.5–90.7	**41.9** 31.1–55.4	**44.0** 37.6–53.9	**33.8** 25.8–48.6	**36.4** 31.6–39.6
Myristica spp.	5	**26.1** 22.7–32.5	**100.4** 73.7–123.6	**54.1** 49.8–60.1	**44.2** 36.4–63.3	**29.0** 19.0–39.2	**39.6** 33.6–46.0
Trichospermum richii	4	**17.4** 11.6–22.2	**198.2** 128.7–270.3	**60.7** 48.9–70.2	**55.7** 42.2–72.9	**31.4** 18.2–49.7	**46.1** 38.5–53.9

* Values represent the mean for two specimens (inner and outer heartwood) from each tree and the range. Species arranged in decreasing order of overall mean for four fungi.
** Incubation period of 8 weeks (12 weeks for *P. coccineus*).
† Reference timbers of known durability included for comparison.

radial measurement varying with each tree. The material was air-dried before a quarter-sawn plank (⅜ inch thick) was removed from each billet for testing.

Two specimens were tested from each tree, for each fungal species. It has been shown in many timbers (Scheffer and Duncan, 1947; Findlay, 1956; Rudman and Da Costa, 1959; Rudman, 1964) that the outermost heartwood is the most durable wood in the tree, and so a sample was taken from this position, as well as one closer to the pith, representing the rest of the heartwood which would be used commercially. The test blocks measured ¾ inch parallel to the fibres, 1⅜ inches radially, and ⅜ inch tangentially, the longest dimension being in the radial direction so as to sample the maximum variation in durability. The sapwood was not normally tested, as it is usually nondurable and can be readily treated with preservatives if necessary. However, in some trees the sapwood-heartwood boundary could not be defined or there appeared to be little or no heartwood, and in these cases sapwood was tested as well as, or instead of, heartwood, inasmuch as this would be the timber used commercially.

Decay Tests

A soil-block method was used in which cylindrical 8-oz glass jars (2¾ inches diameter; 3¼ inches high) with unlined metal screw caps were partly filled with 120 g of forest loam soil at 60% moisture content. Two feeder strips (1¾ × ¾ × 1/16 inch) of beech (*Fagus sylvatica*) sapwood were placed on the soil and, after sterilization, were inoculated with the particular test fungus. After fumigation with propylene oxide (Hansen and Snyder, 1947), two blocks, representing the inner and outer heartwood of the one tree, were placed in each jar, the largest face resting on the fungal mycelium. The percentage loss of weight, as compared with the air-dry initial weight, was used as a measure of the amount of decay.

Four test fungi were used: *Coniophora olivacea* (Fr.) Karst. (DFP 1779) and *Lenzites trabea* Pers. ex Fr. (DFP 8845), both brown-rot fungi, and *Pycnoporus coccineus* (Fr.) Bond. and Sing. (syn. *Coriolus sanguineus* [L. ex Fr.] G. H. Cunn.) (DFP 2544) and *Fomes lividus* (Kalch.) Sacc. (DFP 7904), two white-rot fungi. The incubation period was 12 weeks

for *P. coccineus* and 8 weeks for the other fungi.

After completion of the main decay test, all blocks showing less than 10% weight loss after attack by *C. olivacea* or *F. lividus* were subjected to a further 16 weeks' incubation with these two fungi.

Measurement of Basic Density and Water Uptake

It has been shown for 26 New Guinea timber species (Da Costa and Osborne, 1967) that there is a correlation between percentage weight loss and basic density and, more particularly, between percentage weight loss and water uptake. Therefore, measurements of these two properties were made on two specimens from each tree. The water uptake was measured by standing air-dry blocks, end grain down, in 1/8 inch of water for 24 hours and calculating the increase in moisture content as a percentage of the oven-dry weight. The approximate basic density was calculated using the oven-dry weight and the "green" volume after blocks had been pressure-impregnated with water and allowed to swell for 48 hours.

RESULTS

The basic density and water uptake measurements, together with the decay figures, are presented in Table 2. As some timber species show considerable variation, both among trees and between the two radial positions within a tree, minimum and maximum values have been included, as well as the mean figure. As expected, the outer heartwood was generally more resistant than was heartwood closer to the pith. In 70% of 416 relevant comparisons the percentage weight loss of the outer heartwood was lower.

Palaquium hornei proved extremely durable, being comparable in resistance with the very durable reference timber *Eucalyptus microcorys*. *Intsia bijuga* and *Fagraea gracilipes* also were durable, with several other timbers showing moderate durability. However, the remaining species showed poor resistance, most being highly susceptible.

It can be seen from Table 2 that for each timber species there is a variation in the

amount of decay depending on the particular test fungus, as well as a variation between trees. Because of these variations it is difficult to obtain a meaningful single-figure estimate of the relative decay resistance of the timber species. In Tables 2 and 3 the timber species are arranged in order of decreasing resistance based on the overall mean for the four fungi. However, other criteria may be used, such as the mean amount of decay caused by the most destructive fungus for each timber species, or the mean ranking for each timber (i.e., for each fungal species the timbers are ranked 1–30 in order of percentage weight loss, and the mean of these rankings for the four comparisons is obtained). Mean ranking is useful in cases where the test fungi show different rates of decay, *L. trabea* in particular producing almost consistently lower decay losses than the other three fungi. The advantages and disadvantages of the various methods have been discussed by Da Costa and Osborne (1967). It can be seen, however, that no matter which criterion is used the general order of the timber species does not alter appreciably (Table 3).

Results for the second decay test of the more durable species are shown in Table 4. *Palaquium hornei* and *Fagraea gracilipes* still proved to be durable, whereas the remaining timbers showed quite appreciable weight losses, at least against the white-rot fungus *F. lividus*. An interesting result is that *Intsia bijuga* showed a great increase in weight loss after a further 16 weeks' incubation with *F. lividus*.

As has been stated it was found, after testing had begun, that some timbers consisted of more than one botanical species (see Table 1). It is emphasized that these mixed groups include only species which are regarded as being very similar in many respects, including natural durability. However, the following comments indicate the actual species tested.

Of five trees tested of *Calophyllum* spp., three were identified as *C. vitiense* Turr. (mean percentage weight losses: 20.0, 15.7, 5.4) and two as *C. leucocarpum* A. C. Smith (weight losses: 20.4, 22.1%). The *Canarium* spp. group consisted of three trees of *C. smithii* Leenh., one tree of *C. vitiense* A. Gray, and one tree denoted as *C. sp. aff. C. vitiense,* all five trees

TABLE 3

RELATIVE DECAY RESISTANCE BY VARIOUS CRITERIA

| | PERCENTAGE WEIGHT LOSS | | |
TIMBER SPECIES	Overall Mean	Mean for Worst Fungus	MEAN RANKING*
Palaquium hornei	0.2	0.5	1.0
Eucalyptus microcorys	0.6	1.2	3.5
Intsia bijuga	0.7	2.4	2.2
Fagraea gracilipes	1.4	1.8	4.8
Tectona grandis	1.5	2.6	5.2
Syzygium spp. complex	3.9	6.3	7.0
Eucalyptus obliqua	6.4	14.9	8.0
Dacrydium elatum	6.6	10.1	10.2
Podocarpus neriifolius	7.4	16.6	9.8
Garcinia myrtifolia	7.7	13.2	10.2
Heritiera ornithocephala	7.9	13.9	10.8
Swietenia macrophylla	8.2	19.5	10.5
Palaquium fidjiense	8.7	15.7	12.0
Serianthes myriadenia	13.9	26.0	15.5
Pseudotsuga menziesii	16.6	32.2	16.8
Calophyllum spp.	16.7	22.6	17.5
Casuarina nodiflora	17.4	26.5	16.0
Eucalyptus citriodora	19.7	27.9	18.5
Podocarpus vitiensis	20.0	27.8	18.0
Alphitonia zizyphoides	21.9	33.8	20.5
Agathis vitiensis	25.3	28.7	20.0
Parinari insularum	26.4	31.7	21.8
Terminalia catappa	28.8	40.6	22.8
Gonystylus punctatus	30.2	32.0	24.0
Podocarpus javanica	30.3	35.8	24.2
Pinus radiata (sapwood)	30.9	39.7	24.2
Canarium spp.	33.0	48.0	24.0
Endospermum macrophyllum	39.0	44.0	27.8
Myristica spp.	41.7	54.1	28.0
Trichospermum richii	48.5	60.7	29.2

* For each fungal species, the timbers were ranked 1–30 in order of increasing mean percentage weight loss and the mean of these rankings for the four comparisons was obtained.

showing very similar durability (weight losses: 36.3, 34.9, 28.8; 31.5; 33.3%). Amongst the four trees of *Casuarina nodiflora* sampled was one tree identified as *Gymnostoma vitiense* L. A. S. Johnson, which showed a slightly higher mean percentage weight loss (23.1 cf. 13.0, 18.6, 17.4). However, no conclusions can be drawn from results for one tree of a species. Decay figures were similar for all trees of *Myristica* spp., which consisted of two trees of *M. chartacea* Gillespie (47.7, 39.8%), one tree of *M. castanaefolia* A. Gray (39.1%) and two trees of *M. hypargyrea* A. Gray (40.2, 41.8%). Of five trees tested of the *Palaquium fidjiense* group, two trees were identified as *Palaquium* n.sp., but all showed such similar

decay losses that the two species could not be distinguished on durability in these tests.

In the case of the *Syzygium* spp. complex, apparently a number of botanical species appear very similar in the field, inasmuch as nine different species were received under the trade name of "yasiyasi." On the basis of field characteristics and physical properties of the timber, these species can be divided into two main groups, as shown in Table 5, which includes the mean percentage weight loss for all four fungi for each tree. As there is some variation in the mean percentage weight losses for different trees within a species, and within each group, and as only one or two trees were tested for many of the species, no differentiation

TABLE 4

Decay Losses for Blocks of Durable Timbers Subjected to Second Decay Period

| | MEAN PERCENTAGE WEIGHT LOSS | | | |
| | Fomes lividus | | Coniophora olivacea | |
TIMBER SPECIES	8 weeks	24 weeks	8 weeks	24 weeks
Palaquium hornei	0.5	7.5	0.1	1.3
Eucalyptus microcorys*	0.6	4.2	0.5	1.0
Intsia bijuga	2.4	32.6	0.2	—0.3
Fagraea gracilipes	0.9	6.4	1.8	4.2
Tectona grandis*	2.6	22.6	0.3	2.7
Syzygium spp.	4.0	34.2	2.1	14.3
Eucalyptus obliqua*	6.7	51.1	3.2	14.8
Dacrydium elatum	4.3	32.3	0.3	2.8
Podocarpus neriifolius	4.4	29.4	4.3	13.1
Garcinia myrtifolia	5.6	51.1	1.5	17.9
Heritiera ornithocephala	7.0	44.6	4.2	13.1
Swietenia macrophylla	—	—	3.9	19.2

* Non-Fijian timbers included for comparison.

between the species or groups can be made from these durability results. Although *Acicalyptus myrtoides* belongs to the small-leaf group, tests carried out by the Division of Forest Products, csiro, show that this timber has different strength properties from all other species of yasiyasi. However, as far as natural durability is concerned, it is not possible from the present data to distinguish *A. myrtoides* from the other species, since only one tree was tested.

It may be noticed that *Eucalyptus citriodora* showed rather low decay resistance. This is due to the fact that the specimens tested of two trees were sapwood (mean percentage weight losses 37.4 and 31.1 cf. 6.4 and 4.0 for trees

where only heartwood was sampled). However, since the sapwood in these trees extended for 4–6 inches from the bark, there would be sapwood present in most timber used for commercial purposes, and so the species will show low durability unless heartwood is carefully selected.

The relationships between percentage weight loss, basic density, and percentage water uptake were investigated, first by using a mean value for each timber species, and then by examining relationships within a species. Statistical analyses showed that the correlations between these factors were very similar to those found by Da Costa and Osborne (1967) for

TABLE 5

Decay Losses for Individual Trees of *Syzygium* Species Complex

GROUP	BOTANICAL SPECIES	MEAN PERCENTAGE WEIGHT LOSS FOR EACH TREE			
Yasiyasi 1	*Syzygium nidie* Guill.	5.8	14.9	4.6	
(Small-leaf group)	*Eugenia effusa* A. Gray	1.8	0.6	6.0	0.9
	Acicalyptus myrtoides A. Gray	0.0			
				GROUP MEAN	4.3
Yasiyasi 2	*S. curvistylum* (Gill) Merr. et Perry	2.8			
(Medium-leaf group)	*S. fijiense* L. M. Perry	3.5			
	S. brackenridgei (A. Gray) C. Muell.	3.8			
	Acicalyptus longiflora A. C. Smith	2.6			
	A. eugenioides (Seem.) Drake	6.0			
	A. elliptica A. C. Smith	4.0	1.5		
				GROUP MEAN	3.5
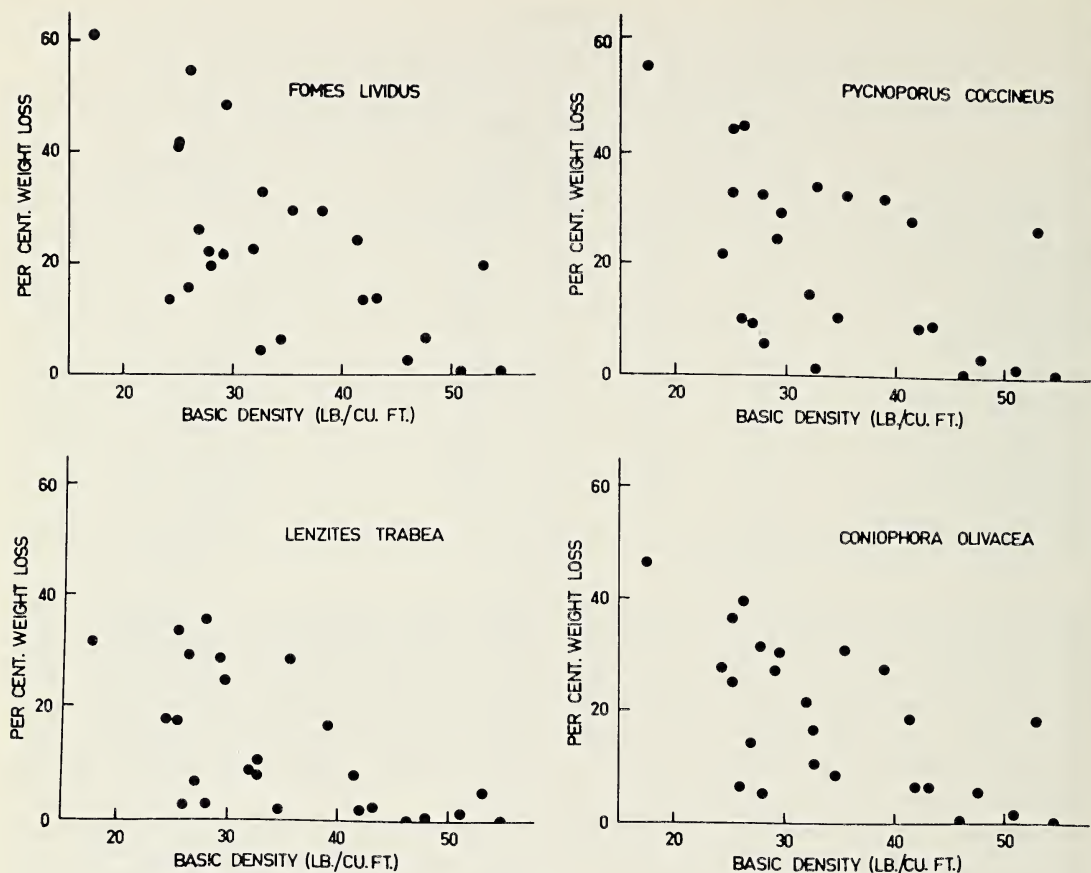
FIG. 1.   Relationship of decay resistance to basic density (species means).

26 New Guinea timbers. The scatter diagrams in Figure 1, using species means, indicate an inverse correlation between basic density and percentage weight loss for each of the four test fungi. It may be argued that, even if absolute losses in weight are identical for blocks of different densities, there would be a spurious inverse correlation of density with percentage weight loss. This possibility has been tested statistically, and it has been shown that the absolute weight loss was not constant for all species, and that there was a small ($r = 0.32$) but highly significant correlation between density and absolute weight loss. As with the New Guinea timbers previously tested, there was a tendency for the more water-absorbent species to be more susceptible to decay (Fig. 2). Inasmuch as there was also a correlation between basic density and water uptake, multiple regression analyses were made. These showed that

for all four fungi, the percentage water uptake was a better predictor of percentage weight loss than was basic density, as is indicated from a comparison of Figures 1 and 2. The effect of water uptake was significant at the 5% level for *F. lividus* and *L. trabea,* and at the 1% level for *P. coccineus* and *C. olivacea,* whereas the additional effect of basic density was not significant for any of the fungi.

The relationship between basic density and decay resistance also held within the timber species for all four fungi. Because it is not practicable to give detailed results, data are presented for four timber species which showed wide ranges of basic density (Fig. 3). Statistical analyses again showed that the correlations between absolute weight loss (and hence percentage weight loss) and basic density were highly significant in each case. The detailed data suggested a similar correlation between
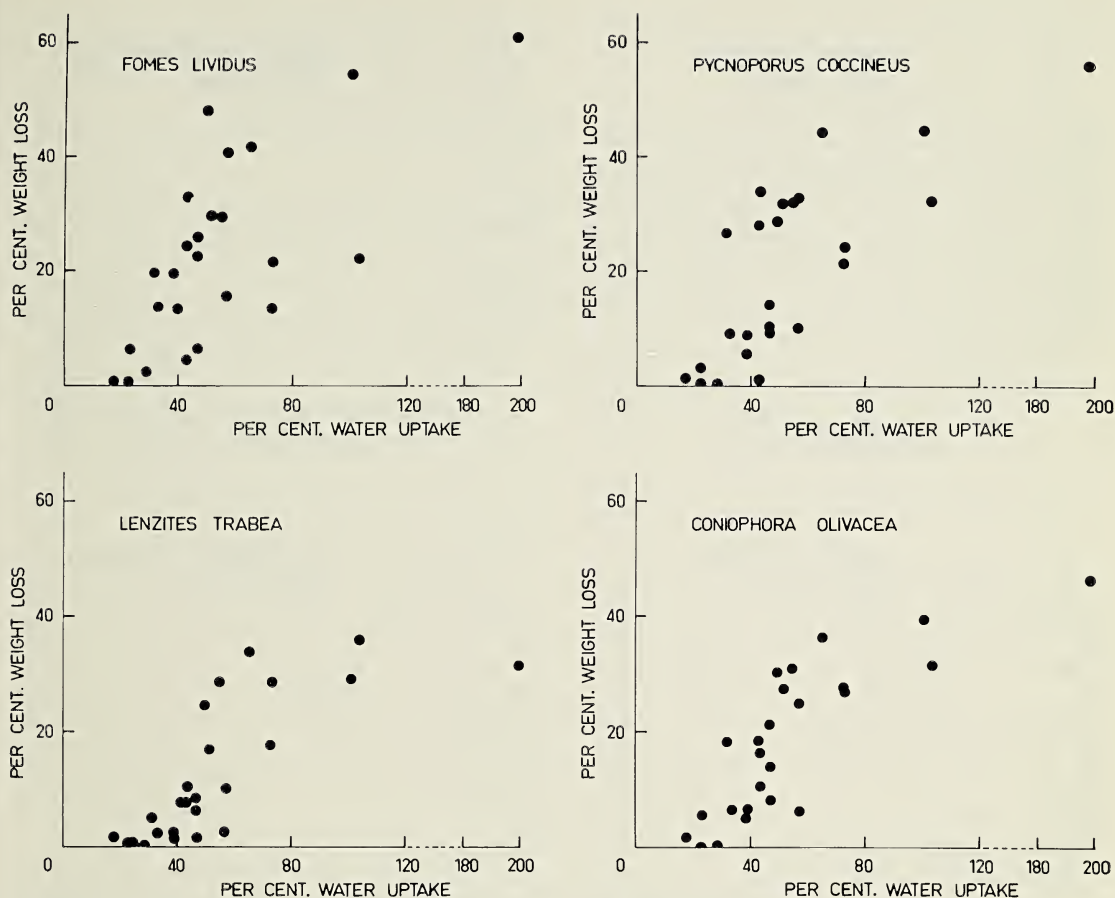
Fig. 2. Relationship of decay resistance to water uptake (species means).

high water absorption and susceptibility to decay within each of these species.

DISCUSSION

From the data in Tables 2, 3, and 4 it can be seen that *Palaquium hornei* proved extremely durable, even after a second, more severe decay test. Its resistance is comparable with that of the highly durable reference timber, *Eucalyptus microcorys,* which is one of the timbers used in Australia for prolonged service in ground contact. *Intsia bijuga* and *Fagraea gracilipes* were also found to be durable, although *I. bijuga* did not show such high resistance after prolonged exposure to *F. lividus.* Specimens of *I. bijuga* from New Guinea have been tested and shown to have comparable durability to the Fijian samples (Da Costa and

Osborne, 1967), and also similar susceptibility to *F. lividus* during a second decay period. This timber has been widely used in ground contact in New Guinea, apparently with satisfactory results, and so the high susceptibility to *F. lividus* may be misleading. *Syzygium* spp. complex, *Dacrydium elatum, Podocarpus neriifolius, Garcinia myrtifolia, Heritiera ornithocephala, Swietenia macrophylla,* and *Palaquium fidjiense* all showed moderate durability, being slightly less resistant than *Tectona grandis,* which does not give extremely long service in the ground although it has an international reputation for durability.

The remaining 16 timbers would probably be too susceptible for use in any situation of high decay hazard, such as ground contact, but a few less susceptible species could possibly give satisfactory service as exposed woodwork,
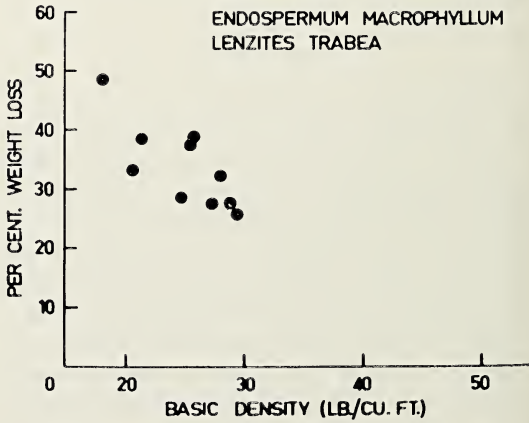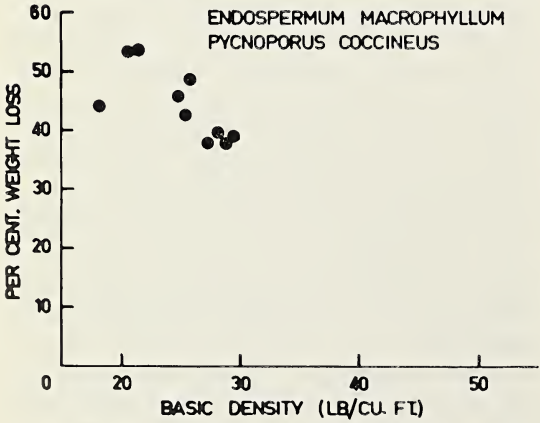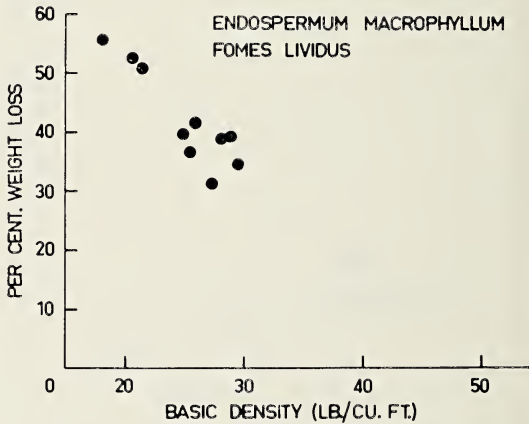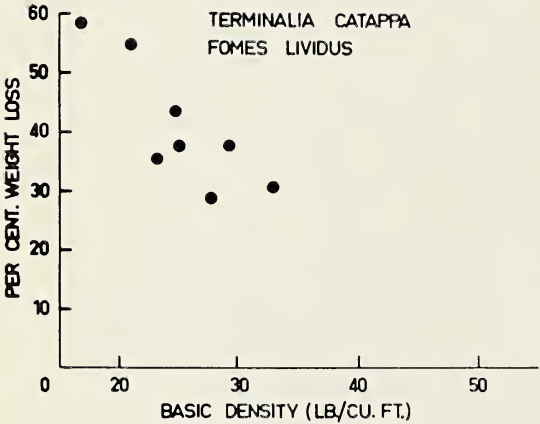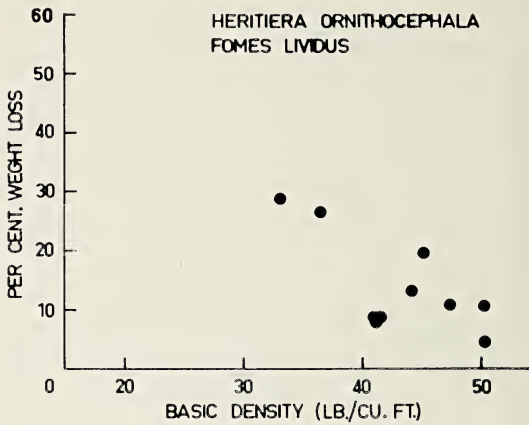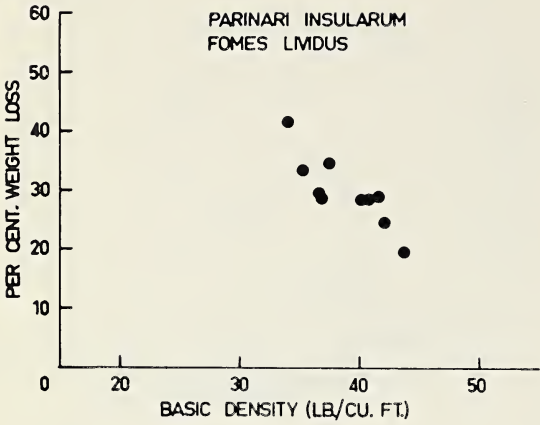
FIG. 3. Intra-specific relationship of decay resistance to basic density (individual specimens).

as does *Pseudotsuga menziesii*. However, those species which are comparable with the highly susceptible *Pinus radiata* sapwood would be unsuitable for external use in humid climatic conditions, unless they were impregnated with a preservative.

Specimens of almost 20 of the species in the present test are, or have been, in graveyard stake tests in Fiji. Although these tests are not complete some comparison can be made between the laboratory and field results (Alston, 1966). In general, there is good agreement between the results of the two types of tests, the timber species ranking in approximately the same order, with only a few exceptions. Specimens of *Garcinia myrtifolia, Palaquium fidjiense,* and *Swietenia macrophylla,* when compared with the other timber species, all showed higher decay resistance in the laboratory tests than they did in the field tests. The reason for this discrepancy is not clear but could possibly be related to rate of wetting. *S. macrophylla,* although not native to Fiji, is an important plantation timber in Fiji, and it is therefore particularly important to note that for this species field test results are not as favourable as laboratory results.

In conclusion, it should be stressed that the relationships obtained in the present tests for the tropical rain forest timbers of Fiji are very similar to those obtained for a group of comparable timbers of New Guinea: notably, that less dense timber species tend to be more susceptible to fungal decay, but, more particularly, that timbers which are highly water-absorbent are more susceptible. It is possible, therefore, that a knowledge of the density of a rain forest timber of which little else is known may be a rough guide to its durability. Again, a majority of trees was shown to have more durable heartwood in the outer zone than in the inner position, although the percentage was

not as high as for the New Guinea timbers (70% cf. 86%).

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NOTES

Notes on the Hawaiian Flora

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IN THIS REPORT on various Hawaiian plants are gathered taxonomic and nomenclatural notes which have accumulated over several years. Certain new taxa, some nomenclatural adjustments, comments on noteworthy collections, and distribution records are presented.

CYPERACEAE

An Additional Species of Cyperus *in Kauai*

Cyperus haspan L. Kauai: Wahiawa Bog, 2 January 1957, *Stone* 1665 (BISH). Det. T. Koyama. New to Kauai; known also (collected once, recently) from Hawaii. Evidently an adventive species; its distribution is very broad.

PAPAVERACEAE

Authority for the Hawaiian Argemone

In his monograph of the genus *Argemone* in South America and Hawaii, G. B. Ownbey cites the Hawaiian species as *Argemone glauca* L. ex Pope, Man. Wayside Pl. Haw., p. 71, pl. 32, 1929, adding the remark "as 'Argemone glauca Linnaeus' in error." This was indeed as Pope published the species. It is manifest from Pope's writing that he believed that *A. glauca* had previously been described by Linnaeus, and he presumably did not check on this assumption. In fact, Linnaeus published no such species. Pope clearly did not intend a new epithet. He also seems to have been unaware of the valid varietal name *glauca* published by Prain, in J. Bot. 33:329, 1895, with Nuttall indicated as the source. However, Pope may have seen this publication, and, retaining in memory the epithet, forgot its rank and place of publication; or

perhaps the glaucous appearance of the plants in question simply suggested the same epithet. We also find Degener, in Plants of Hawaii National Park, p. 164, 1930, using the name *Argemone glauca,* but as a provisional name and hence not a formal nomenclatorial usage; and later in Flora Hawaiiensis (31 July 1958) where, with a long list of synonyms, the name is given as "*Argemone glauca* (Prain) Deg. & Deg. comb. nov." Ownbey considers that this transfer is contrary to Article 32 of the International Code of Botanical Nomenclature (1956 ed.). There seems to be no good reason to invoke Art. 32, however, which in itself offers no reason to consider as incorrect the author citation as suggested by the Degeners. Ownbey himself seems to perpetuate the idea that Pope was "attributing" the name to Linnaeus. This is a practice that has been used at times, but it has nothing to recommend it and in this case is clearly not supported.

We are forced to conclude that Pope's description, although definitely *not* intended as a proposed new name and species, can be taken *as if* he had proposed a new species. He is definitely the first to publish the binomial *Argemone glauca*. He does furnish a good description; since it was published in 1929, he did not have to include a Latin description. He cited no specimens and no holotype; but citation of type is required only after 1 January 1958. He does furnish an illustration. There is no difficulty at all in interpreting his meaning. Consequently we can accept his publication as if it were describing a new species, and thus the correct citation of the name is: *Argemone glauca* Pope, Man. Wayside Pl. Haw. p. 71, pl. 32, 1929 (attributed in error to Linn.).

A neotype should now be chosen for this species. The new combination by the Degeners,

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though technically correct, is superfluous, as priority is by rank.

MALVACEAE

A Synonym for the Hawaiian Hibiscus clayii

In Sister Roe's study of the Hawaiian species of *Hibiscus* (Pacific Sci. 15:3–32, 1961) a new species from Kauai is described and named *Hibiscus newhousei* for its discoverer, W. Jan Newhouse. It was first located in the foothills of the Moloaa Forest Reserve at near 500 ft altitude, and has been collected by I. E. Lane (no. 58-44, 10 November 1958) and by the writer (*Stone* 3420, 3421, 15 April 1960), in company with Tadayuki Kato. I find, however, that this species is synonymous with *Hibiscus clayii* Deg. and Deg. (Flora Hawaiiensis fam. 221, 20 March 1959), which was described from cultivated plants grown from cuttings long since taken from Haiku, Kauai, by Albert Duvel.

Hibiscus clayii Deg. and Deg.

Hibiscus newhousei Roe, syn. nov.

Kauai: Moloaa, mountains ssw of Moloaa, Moloaa stream and waterfall, alt. about 700 ft, 15 April 1960, *Stone* 3420 (flowering), 3421 (fruiting) (BISH).

A small grove of perhaps six plants was found, on vertical rocky banks just above a small waterfall. The trees approached 25 ft in height; some were in flower, and one bore several mature fruits, each in the form of a five-pointed star, the segments follicular, and bearing normal seeds. The flowers were dark-red in color. Associated species included *Cordyline fruticosa, Aleurites moluccana, Pleomele aurea,* and *Eleocharis* sp.

Two Other Recent Collections of Hibiscus

Hibiscus saintjohnianus Roe

Kauai: Na Pali Coast, trail to Kalalau Valley, rim of Hanakoa Valley at about 800 ft alt., 14 August 1961, *Stone, Stern and Carlquist* 3748 (bright orange flowers), 3749 (darker reddish-orange flowers) (BISH).

Hibiscus sp. (perhaps *H. arnottianus,* forma)

Oahu: Waianae Mountains, Palikea trail, alt. 1,500 ft, dry gully, 5 May 1960, *Stone* 3471

(BISH). This collection, taken from a largish tree about 30 ft high, has baffled certain determination because it lacked flowering branches. However, it may be a form of *H. arnottianus,* probably f. *parviflora* Skottsberg. The leaves had light-magenta-colored midribs and veins, purplish and sparingly puberulent petioles (the pubescence stellate), and small subulate reddish soon caducous stipules. The importance of this collection is in showing the species in such a dry locality among almost nothing but weeds.

EUPHORBIACEAE

Two New Taxa in Aleurites

The *kukui* or candlenut tree, *Aleurites moluccana,* is a familiar plant in the Hawaiian landscape, its pale foliage distinct even at long distances and indicating the groves and isolated trees so common at moderate elevations on the Hawaiian mountains and in valleys. It is generally agreed that the plant is one of the aboriginal introductions of the Hawaiians, since it figured largely in the Polynesian culture throughout the high islands of Polynesia, and indeed is a valuable tree for the people of many other Pacific islands. It is known to be planted in groves around many Hawaiian village and temple sites, along trails, and around present-day houses as well. Although surely widespread in Hawaii through natural means, it is also distributed deliberately (or has been in the past), and perhaps also accidentally, since the seeds may be carried easily and perhaps dropped. In other words, it is a plant that is marginally a cultivated plant. Because it was of some importance (for torches, made from the oily seeds; for medicinal purposes, the seeds being somewhat purgative in small doses and violently so in larger ones; and for food, either raw or preferably cooked), the early Hawaiians no doubt took an interest in the trees just as they did in their selections of taro varieties (*Colocasia*), ti varieties (*Cordyline*), bananas, and other plants. This would lead to an observance and to a deliberate selection of unusual forms among the *kukui* trees, as it did with other plants of cultural interest. This selection would tend to perpetuate forms which might otherwise disappear (as for instance at the demise of a particular tree with a remarkable recombination

type), and it would account for the spread of such a remarkable type from island to island.

A few years ago just such an unusual *kukui* was described as a species, *Aleurites remyi* Sherff (Field Mus. Bot. ser. 17:558, 1939) from specimens collected long ago by Jules Rémy (1851–55), apparently somewhere near Kona, Hawaii. Additional collections and good photographs of the leaves were published by Sherff in a later paper (Am. J. Bot. 31:157, pls. 1–3, 1944), and definite localities then were known: Holualoa-Kailua road, North Kona; and a garden in Hilo. A plant was grown from a seed by Dr. Sherff in Chicago. However, according to Mrs. Thomas Jaggar, the Kona tree (or trees) were supposed to have been brought to Hawaii from Kauai (as a nut) and was known locally as the "Kauai" or "mango-leaved" *kukui* or, because of the Kona locality, as the "Kona" *kukui*.

More recently, another unusual *kukui* has been discovered, nearly simultaneously, by Dr. Otto Degener and by Tadayuki Kato on Kauai. Like the "Kona" form, it differs from the common *kukui* in its strikingly different leaves. An individual of this form may be seen on the grounds of Kauai High School in Lihue.

In fact, these two forms have a common tendency, i.e., a relative lengthening of the leaf and reduction or loss of the lateral lobes. In *A. remyi* the lateral lobes are very narrow, the terminal lobe much elongated; in the Kauai High School form the lateral lobes are reduced or absent. In reasonably typical *A. moluccana* proper, the lateral lobes are present and rather broad, and the terminal lobe is not particularly longer. For comparison the sketches in Figure 1 are given. It will be noticed that even in *A. moluccana* proper there is a marked variation in extent of lobing.

In describing *A. remyi* Sherff states: "Several staminate inflorescences have been seen. They appear different from those on *A. moluccana*, with which *A. Remyi* will stand in the section Camirium. . . . However, the floral characters of *A. moluccana* are so lacking in sharp delimitations that much reliance upon them for a distinction from *A. Remyi* seems for the present unwise. *A. Remyi* has slightly smaller petals (for its staminate flowers) and these are often sharply 1-denticulate on each margin close to their expanded distal portion, which in turn is very often irregularly obtuse-denticulate or -lobulate. In *A. moluccana* the tendency is for
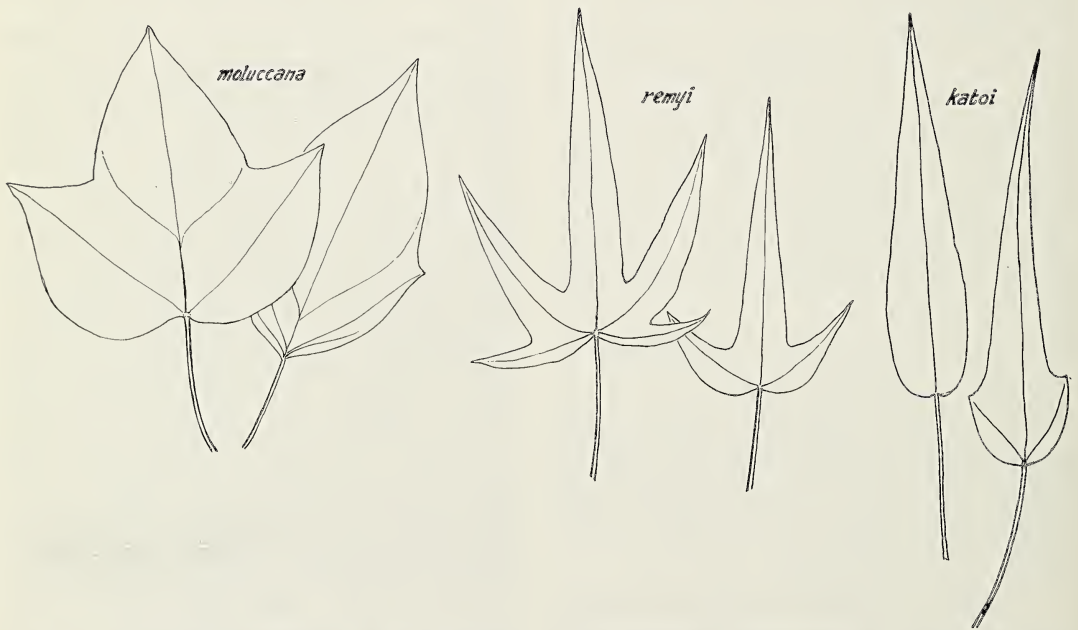
FIG. 1. Leaves of *Aleurites moluccana* in Hawaii. *Left* to *right*: var. *moluccana*; var. *remyi*; var. *katoi*. Not to scale.

the petals to be entire or essentially so." While agreeing that some minor variation in petals does occur it should be added that this is not of any great importance. In short, the discrimination of species is made on the leaf characters alone.

Knowing the somewhat cultivated nature of the Hawaiian *kukui,* and having now a reasonably accurate radio-carbon date from archaeology that shows that the Hawaiian Islands were probably populated rather less than 2,000 years ago, I find it unlikely that *A. remyi* can be considered an endemic native Hawaiian species. In addition, the examination of flowering material of many specimens of *A. moluccana,* including the Kauai High School form, fails to reveal any additional differentiating characters. In conclusion, it appears preferable to treat these forms as subspecific taxa and to suggest that, in fact, they are of aboriginal Hawaiian selection.

The Hawaiian *kukui* trees, then, can be arranged as follows:

Aleurites moluccana (L.) Willd. (syn. *A. triloba* Forst.)

(1) var. *moluccana.* This is the common form not only in Hawaii but elsewhere in the range of the species.

(2) var. *remyi* (Sherff) B. C. Stone, stat. nov.

A. Remyi Sherff, Field Mus. Bot. ser. 17:558, 1939; Am. J. Bot. 31:157, pls. 1–3, 1944.

HOLOTYPE: *Rémy* 600, pro parte (3 sheets, Paris). Although this may be from Kauai, the locality at present known is North Kona, Hawaii. As a common name "Remy's kukui" is suggested.

(3) var. *katoi* Degeners and Stone.

The formal description of this variety will appear in the Flora Hawaiiensis, vol. 7. It is named for Mr. Tadayuki Kato of Kauai High School, who has been very helpful to me and to other visiting botanists. The holotype specimen, taken from the tree on the grounds of Kauai High School in Lihue, is at the Bishop Museum (*Stone* 3427, collected on 15 April 1960). A further specimen collected by Dr. Degener is also available. A suitable common name would be "Kato's kukui" or, alternatively, the "mango-leaved kukui."

ARALIACEAE

A Recent Collection of Munroidendron racemosum

The genus *Munroidendron* Sherff (Bot. Leafl. 7:21, 1953; Am. J. Bot. 43:476, 1956) is of particular interest because it is endemic in Hawaii, consisting of a single species which is very rare. It was rediscovered a few years ago by Tadayuki Kato, of Kauai, and a small collection was made later by a party (the writer, with William Stern and Sherwin Carlquist) that found *Munroidendron* in the Nonou Range not far from the Wailua River, Kauai, on the west side at about 700 ft alt. in the second valley from the south end of the range. The trees were leafless at the time (16 August 1961), but were in flower, the long racemose inflorescences hanging from the rather thick bare branches. A photograph was taken but is not particularly good (Fig. 2). The specimen (*Stone* 3768) is in the Bishop Museum. The single tree seen was on a relatively steep arid slope facing west,

FIG. 2. *Munroidendron racemosum* (Forbes) Sherff; habit of a tree on Nonou Mountains, Kauai (*Stone* 3268).

associated with such species as *Canavalia ga-leata, Sida* sp., *Plectranthus australis, Mucuna gigantea, Aleurites moluccana, Cordyline fruti-cosa, Psidium guajava, Lantana camara,* and other aridity-tolerant plants, many of them weedy introduced species. The tree, with its leafless appearance and numerous dry, decayed branches, had an unhealthy aspect. It should be sought in a season when fruits are ripe so that seeds may be gathered for the preservation of this very interesting species, now perhaps nearly extinct.

APOCYNACEAE

The "Kalaipahoa" Tree of Wahaula Heiau, Hawaii, Is Rauvolfia

During a survey performed by members of a Bishop Museum expedition for the U. S. Na-tional Park Service in Kalapana, Puna, Hawaii in the summer of 1959, a single tree of *Rau-volfia remotiflora* Degener and Sherff was found at Wahaula Heiau, near the coast and not far from Kalapana village. This tree, called "kalai-pahoa," was discovered by S. Konanui and J. Halley Cox. Supposedly in earlier times, during the ascendancy of this heiau, a grove of trees existed, and this one is a remnant of the grove, which was said to contain many kinds of plants useful to the priests. Another collection was made higher on the dry slopes of Kealakomo in native forest (*Stone and Pearson* 3016, alt. 1,400 ft. 9 July 1959, BISH). The same species has previously been recorded from two localities in the Kau District (at Waiohinu and near Kaa-lualu) in Sherff's treatment of 1947 (Field Mus. Bot. ser.). The possibility that the heiau's priests used this plant suggests that they might have had some knowledge of the medicinal properties of the milky sap, which in some spe-cies (especially *R. serpentina* of India) provides an important drug now well known as reser-pine. It would be of interest, therefore, to have the Hawaiian species (which number seven) investigated for this material.

SOLANACEAE

The Identity of Solanum carterianum *Rock*

Rock's description (Indig. Trees Haw. Is. p. 423, 1913), and specimens collected since his discovery of this plant in Hawaii, accord well with a variety of another species: *Solanum verbascifolium* L. var. *auriculatum* (Aiton) O. Kuntze. This appears to have a natural distribu-tion in tropics of both hemispheres, in such regions as Borneo, Sumatra, Java, and Amboina, and has been reported from Tonga. In Hawaii it has been found only in the Waiahole-Waianu Valley on the windward (east) side of the Koo-lau Range of Oahu. Rock listed a vernacular name ("pua-nanahonua") for the plant, which evidently he took as an indication that it was an indigenous species. This is doubtful, how-ever. The very restricted occurrence of this plant in Hawaii, the fact that so many exotic species have been introduced (not all by known persons or at known times), and the remark-able, even reprehensible, lengths to which intro-ducers of foreign plants have gone in distrib-uting alien species, all tend to support the conclusion that this *Solanum* is an exotic, not a native, species. It may have been introduced about 1900. It is easily distinguished from the truly indigenous species of *Solanum* by its ar-borescent habit, dense fulvous tomentum, and rather large bluish-lavender flowers. Endemic species, such as *S. kauaiense* Hillebr., are shrubby, and bear white or purplish flowers. Other introduced species are also mostly herbs or shrubs, and inhabit disturbed areas. *S. ver-bascifolium* is illustrated, under Rock's desig-nation, in Degener's Flora Hawaiiensis.

A New Variety of Nothocestrum (*Solanaceae*)

Nothocestrum longifolium Gray var. *rufo-pilosum* B. C. Stone, var. nov.

Folia magna elliptica usque ad 16–17 × 6.3 cm, laminis costis nervisque pilis rufis tomen-tosis sed ultime glabrescentibus, ramulis glabris.

Leaves large, elliptic, up to 17 × 6.3 cm, the blades, costa, and nerves beneath tomentose with rufous hairs, but at last becoming glabrous; branches glabrous.

HOLOTYPE: Hawaii: between Glenwood and Twenty-nine Miles, in wet forest, 24 June 1929, *O. Degener* 7434 (US).

For its species this is an unusually large-leaved plant, the blades densely rufous-tomen-tose beneath, especially along the midribs and lateral nerves, but in age becoming somewhat glabrate except on the midrib.
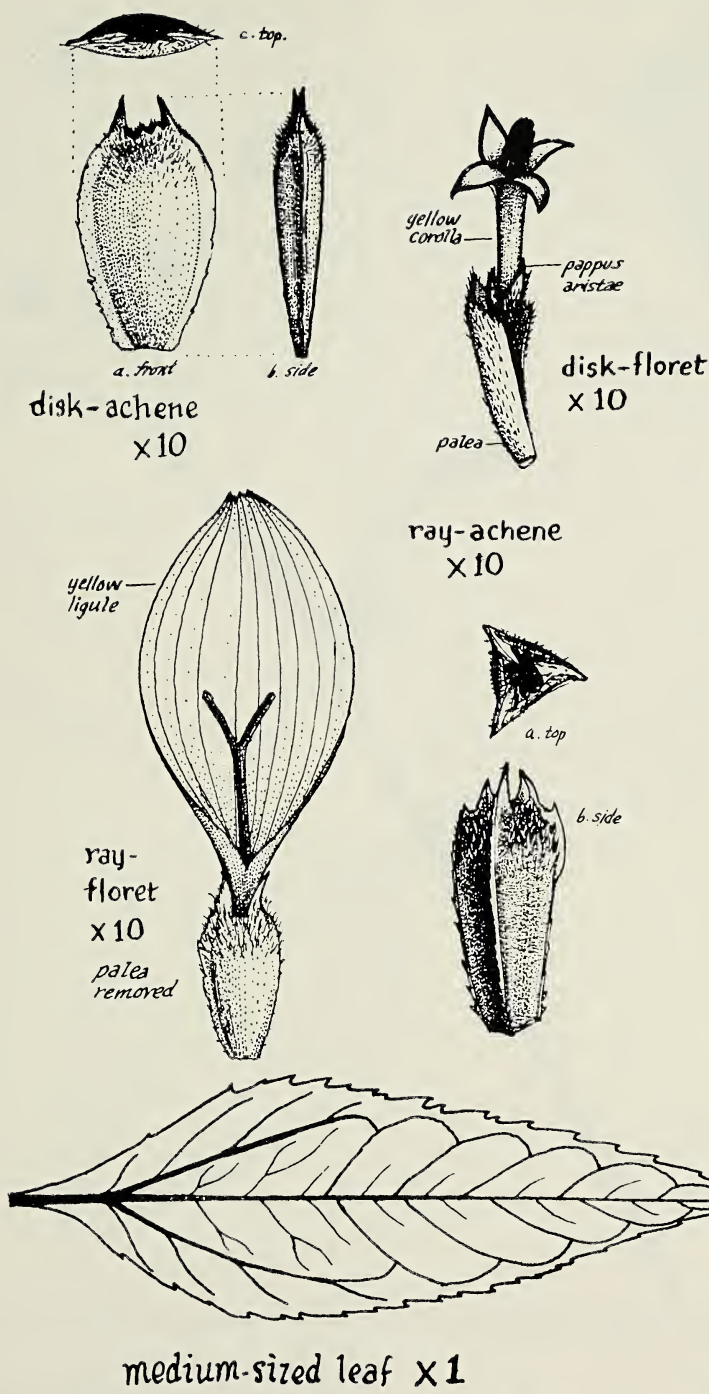
FIG. 3. *Lipochaeta acris* Sherff; leaf, florets (disc- and ray-) and achenes (disc- and ray-). All from Stone 825, Kauai.

achene X 10
dark brown

palea x 10
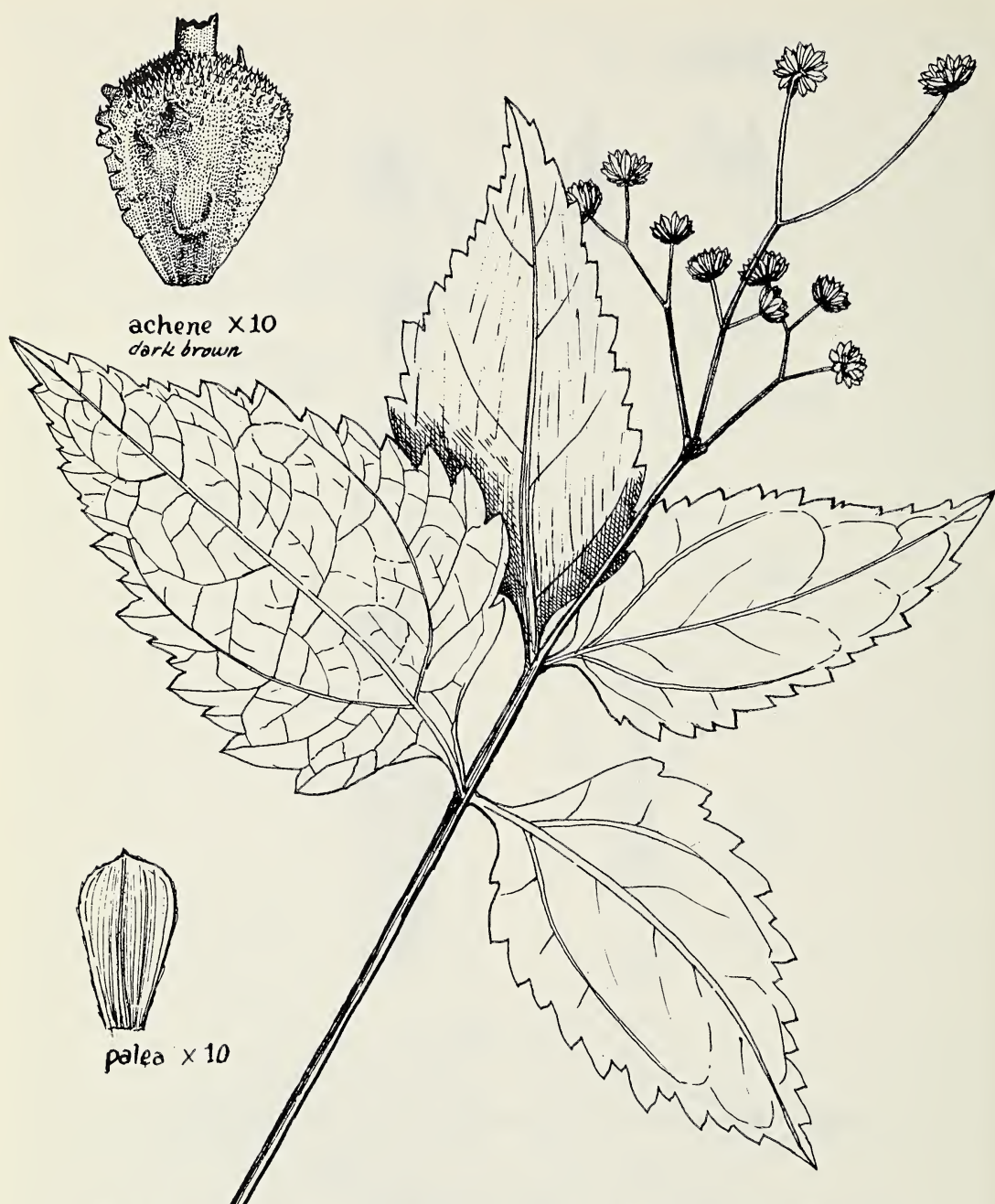
FIG. 4. *Lipochaeta alata* Sherff; habit (× 1), achene and palea. From Stone 760, Kauai.

COMPOSITAE

Rediscovery of Bidens cuneata

In 1959, while I was botanizing on Diamond Head, Oahu, with Dr. Charles Lamoureux of the University of Hawaii, the extremely rare species *Bidens cuneata* Sherff was rediscovered. Previously this had been known only from the original description, based on a single type collection, and had been declared extinct (Dege-

ner, J. Pan-Pacif. Inst. 7(2):3, 1932). But several years ago, Lamoureux and E. T. Ozaki collected it a second time, and the plant appeared to be persisting, not common but not at all extinct. On the last trip about half a dozen individual plants were observed, all within a small area on the northwest rim of Diamond Head (Leahi).

Illustrations of the achenes of two recently collected species of Lipochaeta *(Compositae).*

A number of photographs of herbarium sheets were illustrated in Sherff's monograph (Bish. Mus. Bull. 135, 1935) of the genus *Lipochaeta,* and many good line drawings are found in De-

gener's Flora Hawaiiensis. To these may be added the following:

Lipochaeta acris Sherff

Kauai: Na Pali Coast, Hanakapiai, 500 ft alt., 18 June 1955, *Stone* 825 (BISH).

Habit illustrated in Degener, Flora Hawaiiensis; the additional illustration here (Fig. 3) shows disc and ray florets and disc and ray achenes.

Lipochaeta alata Sherff

Kauai: Na Pali Coast, Hanakapiai, 500 ft alt., 17 June 1955, *Stone* 760 (BISH). Figure 4 shows habit, achene, and palea.

Notes on the Ecology of the Pogonophoran Genus
Galathealinum Kirkegaard, 1956

OLUWAFEYISOLA S. ADEGOKE[1]

THE POGONOPHORAN GENUS *Galathealinum* Kirkegaard, 1956 has a rather wide areal and latitudinal range in the northern hemisphere. It has been recorded from the Arctic Ocean, latitude 69° 32′N (Southward, 1962) to the Celebes Sea, about 1° 50′ north of the Equator (Kirkegaard, 1956). This wide latitudinal range makes the genus an exceptionally good one for examining the ecological factors which control pogonophoran distribution, and one would like to know what ecologic factors may be found to interpret the wide latitudinal range.

Four species have been described within the genus. The first, *Galathealinum bruuni* (the type species) was described by Kirkegaard (1956) from the Celebes Sea in the western Pacific. Ivanov (1961) next described *G. brachiosum* from the Pacific coasts of Canada and Oregon. The most northerly known species, *G. arcticum* was described by Southward (1962) from Thetis Bay, Herschell Island, north of Yukon, Alaska. The writer recently (Adegoke, 1967) described the fourth species, *G. mexicanum* from collections made in the Gulf of Tehuantepec, Mexico. The specimens from the same region earlier listed as *G. bruuni*(?) by Parker (1963:86) belong to this latter species. Apart from these four species, Hartman and Barnard (1960) listed the occurrences of a few large-sized fragments (3–4 mm diameter) of pogonophoran tubes from West Cortes, East Cortes, and Long basins, and from the San Diego Trough off the coast of southern California. These fragments were later referred to the genus *Galathealinum* by Hartman (1961:546). Although specifically indeterminable, these fragments are significant because they are the largest reported tubes of members of this genus.

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ECOLOGY

Because the first records of pogonophoran species were from great depths it was initially assumed that pogonophorans were exclusively inhabitants of abyssal and hadal depths (Kirkegaard, 1956:80). Subsequent records (Ivanov, 1963; Jägersten, 1956; Kirkegaard, 1958; A. J. Southward, 1958; E. C. Southward, 1962; Southward and Southward, 1958, 1963) of pogonophoran species from extremely shallow waters (for example, *Siboglinum caulleryi* Ivanov from 22 m in the Sea of Okhotsk; and *Galathealinum arcticum* Southward from 36 m in Thetis Bay, Herschell Island, Yukon, Alaska) clearly showed that absolute depth is not necessarily a limiting factor in pogonophoran ecology. It is now known that, although a majority of pogonophoran species inhabit abyssal and hadal depths, only a few are characteristically confined to such habitats (Ivanov, 1963:123–126; Southward, 1962:385). Many species are encountered at comparatively shallow depths and a few forms are also known to dwell at bathyal or even sub-littoral depths. A relatively large number, however, thrive in shallow as well as in deep waters. Thus, *S. caulleryi* Ivanov has been recorded from depths ranging from 22 m in the Sakhalin Gulf to depths of about 8,164 m in the Kuril-Kamchatka Trench (Ivanov, 1963:221). According to D. B. Carlisle (see Ivanov, 1963:123), this is the greatest known bathymetric range for any known species of marine organism.

In the light of these presently known depth distributions, Kirkegaard (1958:1087) and

Southward (1962) concluded that the limiting factor in pogonophoran distribution is low water temperature rather than absolute depth. The geographic, latitudinal, and bathymetric distribution of the recorded species of *Galathealinum* discussed below corroborates the views of Kirkegaard and Southward.

The geographic and bathymetric distribution of the four species of *Galathealinum* and of the undetermined species from southern California (Hartman and Barnard, 1960; Hartman, 1961) are shown in Table 1. Figure 1 shows a plot of the minimum depth of occurrence of the species against latitude of occurrence. The data show that there is a direct correlation between these two parameters. The species occupy increasingly greater depths the lower the latitude.

The approximate values of bottom temperatures at the localities where the pogonophoran species discussed here were collected are shown also in Table 1. Temperature values were obtained from published sources, especially from the work of Emery (1954, 1960), Emery and Rittenberg (1952), Kramp (1957), Marmer
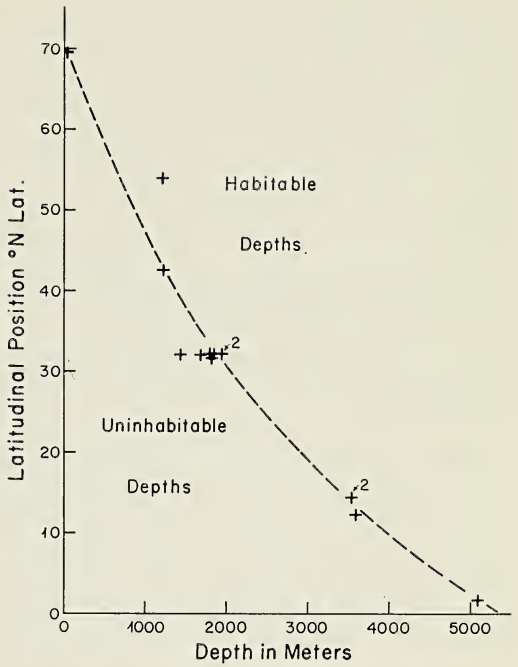
FIG. 1. Relationship between latitudinal position and minimum depth range of species of *Galathealinum*.

TABLE 1

GEOGRAPHIC AND BATHYMETRIC DISTRIBUTION OF SPECIES OF *Galathealinum* KIRKEGAARD, 1956

SPECIES	LOCATION	LATITUDE	LONGITUDE	DEPTH IN METERS	BOTTOM TEMP. °C
Galathealinum arcticum	Thetis Bay, Herschell Island, Yukon, Alaska	69°32′N	138°57′W	36	ca. 0°
Galathealinum brachiosum	west coast of Canada west coast of Oregon	54°23′N 42°40′N	134°41′W 124°29′W	1233–2605	0.61°–0.72°
Galathealinum sp. indet.	East Cortes Basin, southern California	32°21′N 32°16′30″N	118°40′10″W 118°27′55″W	1872 1801	3.13°
	West Cortes Basin, southern California	32°21′N 32°14′N 32°11′N	119°14′W 119°15′W 119°18′W	1924 1923 1668	3.3°
	San Diego Trough	32°19′N	117°26′55″W	1420	—
	Long Basin, southern California	31°55′09″N	119°10′W	1833	2.70°
Galathealinum mexicanum	Gulf of Tehuantepec, Mexico	14°28′N 12°20′N	95°09′W 91°51′W	3529–3557 3596–3642	1.5° 1.5°
Galathealinum bruuni	Celebes Sea	1°50′N	119°30′E	5090–5110	3.8°
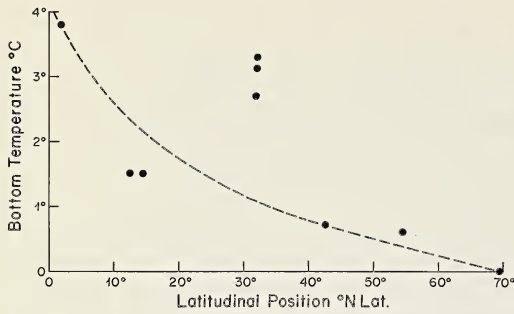
FIG. 2. Relationship between bottom temperatures (°C) and the latitudinal position of species of *Galathealinum*.

(1930), Parker (1963), Sverdrup et al. (1942), and from the Oceanographic Atlas of the Polar Seas, Part II (U. S. Navy Hydrographic Office, 1957). The distribution of bottom temperatures in relation to the latitudinal position of the pogonophoran species is shown in Figure 2. The graph shows that the species closest to the Equator live in comparatively warmer water than those from more northern latitudes. The total temperature range for all the four species, however, is less than 4°C. This narrow range in temperatures, and the fact that these temperatures are from 0°–4°C, seem to explain why these species occupy continuously deeper waters from high to low latitudes. At high latitudes, the temperatures of the water from near the surface to great depths are similar and are within the range of value known at present for species in this genus.

Hence, one could expect that species at high latitudes may occupy the total depth range of the genus provided that other ecological conditions, such as adequate food supplies (as indicated by Kirkegaard, 1956; 1956a), are satisfied.

The occurrence of the undetermined species from southern California at relatively shallower depths than expected (Fig. 1) and in relatively warmer water (Fig. 2) than expected is notable. These basinal occurrences are rather anomalous. More data are needed to explain satisfactorily this particular case.

The diameter of the tubes and the thickness of coarse (external) fibers of the tube walls for the species of *Galathealinum* were examined and found to differ widely. The data are shown in Table 2. The tube diameter and coarse fiber thickness do not show a direct relationship to latitude. Their values increase from the Equator northward, reaching maximum dimensions between 31°55'N and 32°21' N, and decreasing from there toward high latitudes. It is interesting to note that the largest species and the one with the coarsest fibers occur at mid-latitudes (about 31°–32°N) and not at high or low latitudes. But whether this is related to any ecological factors cannot be determined with the data at hand.

Additional data are needed on species distribution, temperature, and nature of bottom conditions to determine whether the indicated relationships are real or merely fortuitous.

TABLE 2

RELATIONSHIP OF TUBE DIAMETER AND COARSE FIBER THICKNESS TO LATITUDINAL POSITION OF SPECIES OF *Galathealinum* KIRKEGAARD, 1956

SPECIES	LATITUDE	DIAMETER OF TUBE (MM)	THICKNESS OF COARSE FIBERS (μ)
Galathealinum arcticum	69°32'N	1.33–1.95	1–2
Galathealinum brachiosum	54°23'N to 42°40'N	2.0–2.6	7–12
Galathealinum sp. indet.	32°21'N to 31°55'09"N	3.0–4.0	—
Galathealinum mexicanum	14°28'N to 12°20'N	1.96–2.5	15–22
Galathealinum bruuni	1°50'N	0.8–2.0	2–4

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Notes on the Systematic Status of the Eels *Neenchelys* and *Myroconger*

GARETH J. NELSON[1]

Neenchelys

BÖHLKE (1960) SUGGESTED that eels of the genus *Neenchelys* possibly have overlapping branchiostegal rays and that, if they did, they should be assigned to the family Ophichthidae. Nelson (1966*a*) described the osteology of *Neenchelys buitendijki*, confirming the presence of overlapping branchiostegal rays, and for this and other reasons referred the genus *Neenchelys* to the family Ophichthidae, subfamily Echelinae. The present report, based on an examination of the holotype of *Neenchelys microtretus*, confirms the presence of overlapping branchiostegal rays in the type species of *Neenchelys*. Like those of *N. buitendijki* (Nelson, 1966*a*, fig. 2*A*), those of *N. microtretus* include six rays articulating with the dorsal portion of the ceratohyal and more than 25 others widely overlapping in the midline.

Myroconger

This genus and the family it represents apparently are known only from the holotype of *Myroconger compressus*. The specimen had been partly dissected, leaving the gill arches exposed, which allowed the following observations to be made: third and fourth upper pharyngeal tooth plates separate; first and second pharyngobranchials absent, the third supporting the tooth plates; basibranchials absent; independent rodlike hypobranchials in arches one–three, those of the third cartilaginous; fourth ceratobranchials not extended anteriorly, not separating the third arches of either side; fifth ceratobranchials apparently absent; ventral parts of the arches not meeting in the midline.

Myroconger has the frontal bones separated by a suture and therefore belongs to the anguilloid lineage of Regan (1912), including the Heterenchelidae, Anguillidae, Moringuidae,

Xenocongridae, Dysomminidae, and Muraenidae (Nelson, 1966*b*). In completely lacking basibranchials, the arches of *Myroconger* differ from those of *Heterenchelys, Anguilla,* and *Moringua,* but resemble those of xenocongrids, *Dysommina,* and muraenids. In lacking a second pharyngobranchial they are unlike xenocongrids, but resemble *Dysommina* and muraenids. Like that of *Dysommina* the fourth arch of *Myroconger* is not appreciably enlarged and "pharyngeal jaws" like those of muraenids do not occur. Thus, the arches of *Myroconger* are most like those of *Dysommina*. The most notable differences include the presence in *Myroconger* of third hypobranchials (a primitive feature) and the apparent absence of fifth ceratobranchials (an advanced one).

What could be learned of the pharyngeal musculature also suggests a relationship with the more advanced eels of the anguilloid lineage, for a subpharyngealis occurs, as it does at least in *Moringua, Kaupichthys,* and muraenids, and retractor muscles have a small area of origin on the vertebral column, foreshadowing the large area of origin in some muraenids (Nelson, 1967).

These observations of *Myroconger* complete a review of gill arch structure for the families of anguilloid eels (Nelson, 1966*b*). Within this group, on the basis of gill arch structure there seem to be three main lines of specialization, each characterized by reduction of the gill arch skeleton: one leads toward the Moringuidae, another toward the Muraenidae, the other toward the Cyemidae. If the anguilloid eels are given the status of a suborder, these lines of specialization could be given the status of superfamilies. However, on the basis of gill arch structure alone it is difficult to distinguish between generalized members of these different lines, or to decide which if any Recent forms can be considered generalized muraenoids. Consequently, the following synopsis is offered more as a working hypothesis than as a final classification:

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Caudal fin continuous with dorsal and anal; no pelvic fins; frontal usually paired . . . . suborder Anguilloidei

a. Jaws not produced; gill arch skeleton including at least rudimentary basibranchials . . . . superfamily Anguilloidae (including families Heterenchelidae, Anguillidae, Moringuidae)

b. Jaws not produced; gill arch skeleton without basibranchials . . . . superfamily Muraenoidae (including Xenocongridae, Dysomminidae, Myrocongridae, Muraenidae)

c. Jaws produced; gill arch skeleton with or without basibranchials . . . . superfamily Nemichthyoidae (including Serrivomeridae, Nemichthyidae, Cyemidae)

Observations on type specimens were made through the courtesy of Dr. P. H. Greenwood at the British Museum (Natural History) while I was on an NSF postdoctoral fellowship.

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Record of a Lancelet from Hawaii

L. G. ELDREDGE[1]

THE SPECIES *Epigonichthys maldivensis* (For-
ster Cooper, 1903) was originally described
from 45 Maldive Island specimens as *Hetero-
pleuron maldivense*. Parker (1904) also re-
corded 12 other specimens from the same island
group. Both Forster Cooper's and Parker's
specimens were collected from depths of 15–20
fathoms. No further specimens have been
found. The generic status is somewhat confused,
for in Franz's (1922) generic revision of the
cephalochordates, the species appears as *Asym-
metron maldivense*. However, in the same year
Hubbs (1922) listed the species in a world-
wide review of the group as *Epigonichthys mal-
divensis*, establishing it in his asymmetrical-
form family, Epigonichthyidae. (In neither
paper is reference given to the other one.)

The single specimen from Hawaii was col-
lected alive by R. E. Johannes and the author
via the "Pele" dredge through coarse sand off
Barber's Point, Oahu, at a depth of 16–20
fathoms on March 18, 1962. This report con-
stitutes the first record of a lancelet (amphi-
oxus) in Hawaiian waters.

With two exceptions its characteristic mea-
surements fall within the ranges of Forster
Cooper's specimens as analyzed by Punnett
(1903) as well as within those given by Franz
(1922), who used a combination of the Forster
Cooper-Punnett and the Parker characteristics.
The following table compares the characteristics
of these specimens.

The two features which differ from those
previously described are the greater number of
myotomes from the anus to the tip of the tail,
and the smaller number of gonads, a peculiarity

CHARACTER	PUNNETT (1903)	FRANZ (1922)	OAHU SPEC.
Length (mm)	18–30	16–30	23
No. Myotomes			
Total	70–76	70–76	73
Head to atriopore	42–46	45	43
Atriopore to anus	15–17	16	15
Anus to tip of tail	11–14	12	15
Gonads	23–30	25	18

which might be explained by the intermittent
location of the 18 gonads lying irregularly
beneath at least 22 myotomes. Forster Cooper's
original figure shows what looks like at least
one gonad per myotome.

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Guam. Manuscript received April 3, 1967.

News Note[1]

THE ADDITION OF seven tide stations in Chile will give Alaska, Oregon, Washington, Hawaii, and many Pacific Basin nations up to two or more hours additional warning time when a destructive tsunami is generated off the Chilean coast.

This was disclosed by Mark G. Spaeth of the Environmental Science Services Administration's Coast and Geodetic Survey.

Spaeth, a geophysicist in the Office of Seismology and Geomagnetism, made the disclosure following his return from an 18-day trip to South America designed to improve the Tsunami Warning System in the Pacific. The System is operated by the Coast and Geodetic Survey in Honolulu.

Spaeth conferred in Valparaiso with officials of the Chilean Hydrographic Institute, and agreement was reached to supply reports on tide conditions from seven additional tide stations to the C&GS Honolulu Observatory, which issues the warnings. Until now, there were only two participating tide stations in the Tsunami Warning System along the entire coast of South America—at Valparaiso, Chile, and Callao, Peru.

"This should greatly reduce the time needed to confirm the existence of tsunamis originating along the South American coast," said Spaeth, "and provide up to two or more hours additional warning time to people throughout the Pacific Basin when a destructive wave is generated."

A 1960 tsunami off the Chilean coast caused deaths and extensive damage in Chile, Hawaii, the Philippines, Japan, and Okinawa. In spite of six hours' warning, 61 persons were killed in the Hawaiian city of Hilo. All Chilean coastal towns between the 36th and 44th parallels were destroyed or severely damaged by earthquake and the ensuing tsunami. In California, a half-million dollars' damage was caused to harbor installations and ships at Los Angeles, San Diego, Cresent City, and Half Moon Bay. Crescent City was also the scene of widespread destruction from a tsunami generated by the March 1964 earthquake in Alaska. Eleven persons lost their lives in this community.

Spaeth also conferred with scientists in the Panama Canal Zone, Peru, and Ecuador. As a result, further steps to strengthen the Warning System may be taken in these areas.

"Tsunami" is the Japanese name for a seismic sea wave, the destructive oceanic offspring of earthquakes and volcanic eruptions. Although frequently, and mistakenly, called tidal waves, they are not related to the tides.

The phenomenon is a series of ocean waves, not unlike those made when a pebble is dropped into a pond, which travel up to 600 miles or more per hour. In the open ocean the crests of the waves are sometimes hundreds of miles apart and always only a few feet high. As the tsunami nears the coast, the speed diminishes and the waves increase in height. They cannot be seen from the air, nor felt aboard ships in deep water. This is why tide stations are essential in the Warning System—to report to the System Headquarters at Honolulu any change in water level, following large earthquakes, that could indicate a tsunami has been generated. The Honolulu Office in turn alerts Civil Defense agencies in communities the tsunami may strike so the low-lying areas can be evacuated.

The Tsunami Warning System was established by the Coast and Geodetic Survey following the disastrous Aleutian tsunami of April 1, 1946, which struck the Hawaiian Islands without warning, leaving 159 persons dead and about $25 million property damage. But this was the last tsunami to strike Hawaii without warning, because the Coast and Geodetic Survey developed and installed a network of seismographs around the Pacific to detect the earthquakes which cause tsunamis.

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[1] From: Earthquake Information Bulletin 1(3):1–4 (1967).
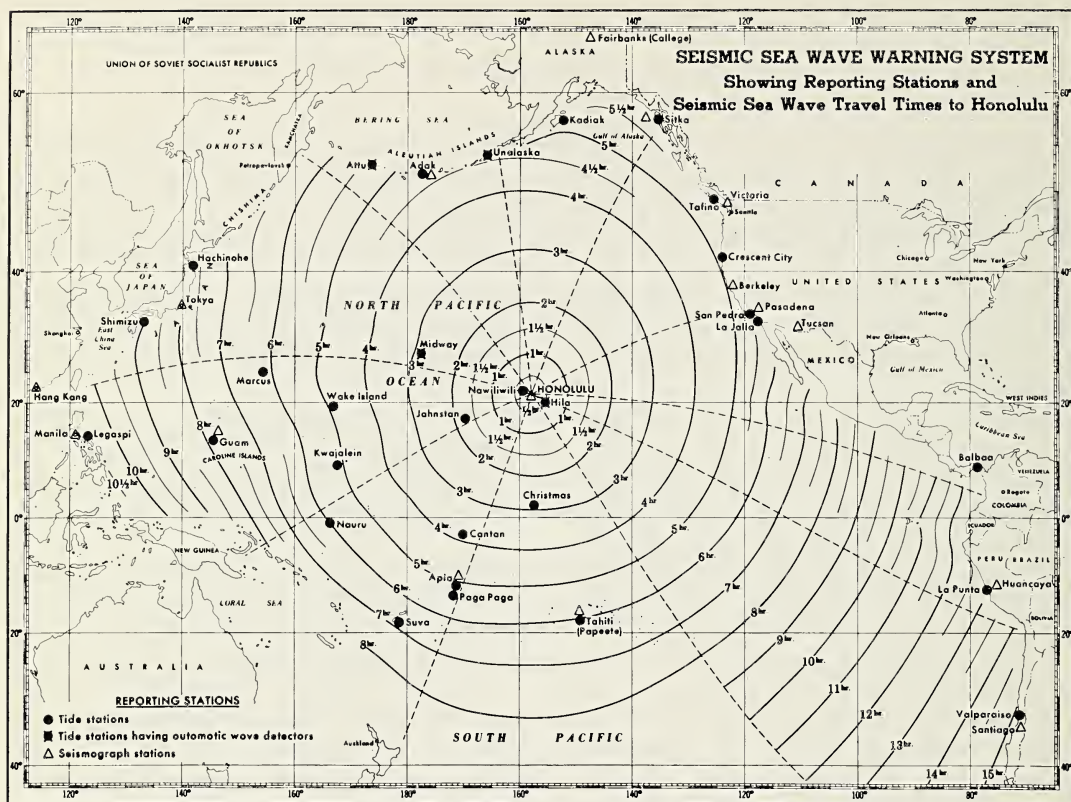
Since only a very few of the thousands of earthquakes which occur annually cause tsunamis, it was also necessary to include tide stations in the Warning System to detect the waves. The Coast Survey's network of tide stations was expanded and a tsunami detector was developed which filtered out tidal and wind waves. Tsunami traveltime charts were prepared to provide a rapid and easy method of estimating tsunami arrival times at tide stations in the Warning System. The military services and Federal Aviation Agency initially provided communication facilities. As the Warning System expanded, facilities of the Department of Defense and foreign governmental agencies were utilized.

The Warning System began operation in August, 1948. Initially it consisted of the C&GS seismological observatories at College and Sitka, Alaska; Tucson, Arizona; and Honolulu, Hawaii; and nine tide stations. Today the System has 17 participating seismic observatories and 30 tide stations (see map).

In addition to the United States and Chile, the Tsunami Warning System now provides warnings to Tahiti, Japan, Taiwan, Fiji, Hong Kong, New Zealand, Western Samoa, Canada, and the Philippines.

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